THE FEEDING ECOLOGY OF AND CARBON AND NITROGEN BUDGETS FOR *ENGRAULIS CAPENSIS* IN THE SOUTHERN BENGUELA ECOSYSTEM.

BY

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CONTENTS

DEDICATION

This thesis is dedicated to my wife, Tania Adele for her patience, understanding and unfailing support and to my parents Ted and Maureen for providing me with my education and for their confidence in me and my work.

DECLARATION

All field samples discussed in Chapter Two were collected by myself, except those during May 1983, which were collected by Mr. H. Verheye. All counts, identification and processing of the samples were conducted by myself. The data base used to manipulate the data collected was developed by Mr. J. Roberts of Scientific Computers under my direction. The methods employed to collect wild anchovy and maintain them in the laboratory evolved from ideas that I discussed with Drs. L. Hutchings and C. L. Brownell and Mr. D. Horstman. All the microbial analyses discussed in Chapter Three were carried out by myself under the supervision of Dr. D. Muir. All experiment were designed and conducted by myself with assistance from the following people:
Mr. K. P. Findlay acted as my laboratory assistant for some of the experiments described in Chapter Four while he was carrying out an Honours project under my supervision.
Dr. T. Probyn trained me in the methods required to measure the ammonia, urea and dissolved organic nitrogen content of the water samples discussed in Chapter Six and provided assistance during the experiments discussed in Chapters Five and Six.
Dr. L. J. Seiderer carried out the enzyme assays discussed in Chapter Six.

I lay claim to all experimental design, concepts, hypotheses, discussion and conclusions contained in this thesis.

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ABSTRACT

The two main schools of thought regarding the diets of intermediate microphagous clupeids are: A) that they are herbivorous and B) that they are omnivorous, but consume mainly zooplankton. The former view has been employed to explain their abundance in upwelling areas, since their purported ability to efficiently utilise the primary producers shortens the pelagic food chain to 1 or 2 links. The literature concerning the trophic ecology of some commercially important clupeids is reviewed and it is concluded that few are true phytophagists. Most are omnivorous and derive the bulk of their energy from zooplankton. Results indicating that these fish are herbivorous are largely due to inadequate sampling strategies and analytical techniques.

The results of field work show that *Engraulis capensis* feeds selectively upon meso- and macro-zooplankton. Laboratory experiments supported these findings. Prey are selected on the basis of size and particulate feeding is the dominant mode of intake when the fish are presented with a mixed size assemblage of prey. *Engraulis capensis* cannot filter feed on particles less than 0.200mm maximum dimension, and there is a threshold size of approximately 0.700mm when feeding behaviour switches from filter to particulate feeding. Particulate feeding produced faster clearance rates than filtering, and the Cape anchovy feeds at maximum efficiency over most of their prey size spectrum.

There are significant log-linear fits between the respiration rates and swimming speeds during both filter and particulate feeding activity. Particulate feeding is more cost effective than filtering in terms of rate of energy intake relative to expenditure. A mean RQ value of 0.915 ± 0.183 indicates that *E. capensis* utilises protein directly as a major source of metabolic fuel. *E. capensis absorbs zooplankton carbon and nitrogen more efficiently than the phytoplankton counterparts* (C_z = 77.88 ± 7.22% C_P = 50.57 ± 0.69%; N_z = 87.38 ± 4.28% N_P = 83.21 ± 1.80%), indicating that the former are a superior food source. A constant portion of the ingested and absorbed N are excreted (41.5% and 47.8% respectively) and it is estimated that 100mm anchovy require a maintenance ration of 2.17 mg N. g dry wt^{-1}. day^{-1}.

The carbon and nitrogen budgets developed during this study differ from those reported in the literature for planktivores, since they are derived from empirical relationships rather than a purely theoretical approach. The model indicates E. capensis cannot maintain itself in the Southern Benguela by filterfeeding alone. It can do so by particulate feeding upon the patchily distributed mesozooplankton, and supplementing this income by filterfeeding upon dense aggregations of phytoplankton and microzooplankton. In conclusion, E. capensis is well adapted to efficiently utilise its preferred zooplankton prey, which are patchily distributed in the Southern Benguela.

CHAPTER ONE

Are clupeid microphagists herbivorous or omnivorous? A review of the diets of commercially important clupeids, with special reference to *Engraulis capensis* and *Sardinops ocellatus*.

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The diets of commercially important fish have been of interest to fisheries biologists since the instigation of marine research. Food is a principal factor regulating growth, abundance and migration and data concerning the trophic habits and ecology of a species can enhance our ability to manage that resource.

Primitive fishes were macrophagous - preying upon items 1/2 -1/20 of their own body length (Manooch 1973). The advent of the teleosts during the Ordovician Period, with their improved swimming ability and more complex jaw structure, led to a divergence in evolutionary development towards microphagy (Marshall 1965; Durbin 1979). This enabled teleosts to utilise the plankton populations that abound in the world's coastal waters. The Clupeiformes may be divided into four groups on the basis of anatomical and behavioural adaptations which refect an increase in specialisation toward microphagy (Table 1).

Particulate feeding microphagists such as *Etrumeus whiteheadi* are facultative planktivores which are capable of supplementing their diet with alternative food sources, e.g. pelagic fish larvae (Durbin 1979; Wallace-Fincham 1987; James unpubl. data). Their jaw structure has become adapted for "sucking in" their prey with the surrounding water rather than grasping it (Durbin 1979). The prey is usually ingested intact (Leong and O'Connell 1969: O'Connell 1972: O'Connell and Zweifel 1972: Werner 1974: Werner and Hall 1974; Confer and Blades 1975; Angelescu 1982; Wallace-

Fincham 1987; Chapters two and four) and their teeth have been resorbed by the jaw (Durbin 1979).

The true filter feeders, such as *Cetengraulis mysticetus* (Bayliff 1963) and *Brevoortia tyrannus* (Durbin and Durbin 1975) represent the most specialised microphagists and are obligate planktivores (Durbin 1979). They have developed filtering mechanisms on their branchial arches (Peck 1894) which sieve out phytoplankton and microzooplankton as the fish cruise through the water with their mouths agape. The jaw structure has become modified such that the mouth acts as a mouth-reduction cone similar to those employed on high speed plankton samplers, to facilitate the flow of water through the filtering mechanism and to minimise the "bow wave" effect caused by pushing a fine mesh through water (Tranter and Smith 1968; Gibson and Ezzi 1985; Chapter four). The alimentary canal has also been extended in these fish to cope with the continuous influx of microscopic material and vegetable diet (Marshall 1965; Nelson 1967; 1970; Blaxter and Hunter 1982).

Most clupeids are intermediate between the two above mentioned extremes, being able to particulate feed upon the mesozooplankton, yet also possessing a filtering mechanism, which, although somewhat coarser than that of a true filter feeder (Durbin and Durbin 1975; Chapter four) enables them to collect the larger elements of the phytoplankton and microzooplankton populations (Radovich 1952; Hand and Berner 1959; Leong and O'Connell 1969; de Mendiola

1971; Janssen 1976b; 1978; Holanov and Tash 1978; Koslow 1981; Angelescu 1982; Angelescu and Anganuzzi 1981; Chapter two). There is a threshold size at which feeding behaviour switches from filtering to particulate feeding or *vice versa* (Leong and O'Connell 1969; Hunter and Dorr 1982; Chapter four) and it has been suggested that this is governed by the energetic constraints of output versus gain of each feeding mode on a particular prey size.

Their low trophic position make intermediate microphagists important controllers of the energy flow to higher predators (Cushing 1978; Durbin 1979; Chapter two). They abound in the fertile upwelling areas of the world where they form the world's largest fisheries: the Peruvian anchoveta fishery yielded 12 000 000 tonnes p.a. at its peak (de Mendiola 1974). There has been a great deal of interest in these fishes and many workers have attempted to determine their diet and rationalise their tremendous abundance in upwelling regions. This has often proved futile and caused considerable debate; in some cases the controversy has arisen from two researchers arriving at different conclusions from the same samples (Lewis 1929; Parr 1930). Ryther (1969), supported by Longhurst (1971), Walsh (1975, 1981) Durbin (1979) and Blaxter and Hunter (1982), proposed the most popular theory that clupeid microphagists are plentiful in upwelling regions due to their ability to bypass one or two links in the pelagic food chain and feed directly upon the primary producers. Blaxter and Hunter (1982) concluded that filter feeding upon phytoplankton

dominated the trophic habits of clupeids in regions where upwelling was a persistent oceanographic feature, e.g. Peru and the South African west coast, while zooplankton was important in more stable , less productive areas, such as the Southern Californian coast. However, no one has produced adequate data to substantiate these arguments and more recent studies tend to refute them (Cushing 1978; Koslow 1981; Angelescu 1981, 1982; Angelescu and Anganuzzi 1981; Chapter two). The object of this chapter is to review and put into perspective the historical data and resulting arguments concerning the trophic ecology of clupeid microphages.

FEEDING BEHAVIOUR

The feeding modes of clupeid microphages have been adequately described from laboratory studies (Blaxter and Holliday 1958; Leong and O'Connell 1969; Rosenthal and Hempel 1970; O'Connell 1972; O'Connell and Zweifel 1972; Durbin and Durbin 1975; Janssen 1976; 1978; Holanov and Tash 1978; Gibson and Ezzi 1985; Chapter four). Loukashkin (1970) and Schülein (pers. comm., see appendix A) have described filtering behaviour and particulate feeding frenzies from field observations for *Engraulis mordax* and *Sardinops ocellata* respectively. In addition to the filtering and particulate feeding modes, some species display a tendency towards iliophagy (Bayliff 1963; de Ciechomski 1967b; Chapters two and four) and

TABLE 2. Threshold concentrations of prey required to elicit filter feeding activity in three important clupeids.

SPECIES	TYPE	FOOD SIZE µm	CONCENTRATION No/l	µg/l (dry wt)	µgC/l	REFERENCE
Brevoortia tyrannus	*Thalassiosira rotula*	21.6	1400 000	-	84.0	Durbin and Durbin 1975
	Ditylum brightwelli	79.0	75 000	-	75.0	
			78 500	-	78.0	
	Acartia tonsa	1200.0	15.7	-	36.9	
			9.5	-	22.3	
			10.8	-	25.4	
Engraulis mordax	Gymnodinium splendens	40.0	151-328	1.8-3.8	-	Hunter and Dorr 1982
	Artemia salina nauplii	433.0	5-18	8.5-31.0	-	
	E. mordax	1340.0	1-2	30-60	-	
Engraulis capensis	*Chaetoceros* species	11.0-114.0	506705	59.87	18.62	Chapter four
			574001	67.85	21.10	
	Brachionus plicatilis	158.0	56.1	24.1	8.37	
	Artemia salina nauplii	540.0	4.5	5.1	2.17	
			4.5	5.1	2.17	
			7.2	8.2	3.49	

are also capable of capturing floating prey (Chapters two and four).

Food concentrations required to initiate and terminate feeding activity have been determined for several important species (Table 2). Particulate feeding *E. capensis* responded to very low concentrations of prey (< 1 copepod/3.5m³ of water, Chapter four). Durbin and Durbin (1975) and James (Chapter four) observed an inverse relationship between the prey size and the density or biomass required to initiate filtering. Hunter and Dorr (1982) found that while the density threshold required to initiate filtering in *E. mordax* was inversely related to prey size, that for biomass was positive correlated.

Some authors have indicated that there may be a density threshold governing the change in feeding mode. O'Connell and Zweifel (1972) observed that *Scomber japonicus* filter fed upon high densities of large particles but switched to particulate feeding when the concentration fell below a threshold level. Using an artificial feeding device, Janssen (1976a) attempted to demonstrate that filtering was more effective for capturing copepods than particulate feeding, especially when prey densities were high. However, his findings were inconclusive since the behaviour of his device did not resemble that of foraging intermediate microphagists. Gibson and Ezzi (1985) described a threshold for *C. harengus* feeding on *Artemia salina* nauplii but James (Chapter four) argued

that this behaviour was an artefact of the size of prey used in the experiments, as it fell into the range of prey sizes where the fish switch from filtering upon microzooplankton and phytoplankton to particulate feeding upon mesozooplankton. Particulate feeding invariably produced the highest ingestion rates during laboratory experiments and observations indicated that it dominated filtering behaviour (Leong and O'Connell 1969; O'Connell 1972; Holanov and Tash 1978; Chapter four). Several laboratory and field studies have emphasised the flexibility of the feeding behaviour of intermediate microphages when presented with mixed size assemblages of potential prey (O'Connell 1972; Holanov and Tash 1978; Koslow 1981; Gibson and Ezzi 1985; Chapters two and four).

FEEDING PERIODICITY

Planktivores generally display diel feeding and activity cycles, foraging either during the day (Yoneda and Yoshida 1955; Davies 1957; Baxter 1967; Loukashkin 1970; de Mendiola 1971; Volkova 1973; Koslow 1981; Gibson and Ezzi 1985; Wallace-Fincham 1987; Valdes *et al* 1987) or at twilight and night (Lissener 1925 and others reviewed in Woodhead 1966; Hobson 1968; Longhurst 1971; Janssen and Brandt 1980; Angelescu 1982; Chapter two). Few studies have observed feeding during both day and night (Hand and Berner 1959). *Clupea harengus*, the most studied clupeid, has been

identified as a twilight forager. Peak feeding occurs at dusk and dawn in the upper layers with a decrease in intensity during the darkest hours (Woodhead 1966; De Silva 1973). Little feeding occurs during the day when the fish are found in tight shoals at depth or on the seabed(Lissner 1925; Jesperson 1928; Muzinic 1931; Blaxter and Holliday 1958; Bityukov 1959; Woodhead 1963). Direct observations from a submarine have confirmed these findings (Radakov and Solov'ev 1959; Zaitsev and Radakov 1960; Solov'ev 1961; Radakov 1973).

Data concerning the feeding periodicity of other marine clupeids is scarce and conflicting. Baxter (1967) classified anchovies as daytime feeders and this generalisation appeared to apply to many species; *Sardinops melanosticta* (Yoneda and Yoshida 1955); *Sardinops ocellatus* (Davies 1957); *E. mordax* (Loukashkin 1970; Koslow 1981); *Engraulis ringens* (de Mendiola 1971); *Etremeus whiteheadi* (Wallace-Fincham 1987) and *E. capensis* (Valdes *et al* 1987). Longhurst (1971) described *E. mordax* as a nocturnal forager, with peak feeding activity at dusk and dawn and stated that peak feeding was accompanied by the ascent and dispersion of the shoals. Angelescu (1982) and James (Chapter two) described similar feeding and shoaling patterns for *Engraulis anchoita* and *E. capensis* respectively and were able to associate the different feeding modes with levels of feeding activity and shoaling states. Filter feeding predominated when trophic activity was low, usually during the day when the fish were aggregated in

dense shoals at depth, while mixed, mainly particulate, feeding behaviour was associated with the ascent and dispersion of the shoals at dusk. Similar shoaling patterns, possibly associated with feeding, have been described for several other species (Blackburn and Tubb 1950; Furnestin 1953; Owatari *et al* 1953; Nomura 1959, 1960; Cushing 1960; Postuma 1960; Balan 1961).

Indirect evidence supporting the argument that clupeids are twilight or nocturnal foragers is abundant. Marshall (1965) and Lythgoe (1966) stated that the eyes of fishes were adapted to provide maximum sensitivity and contrast perception in an environment characterised by low illumination, poor visibility, and monochromatic light. O'Connell (1963) demonstrated that the eyes of *E. mordax* and other pelagic species were well adapted for visual predation in twilight conditions. The northern anchovy also preferred lower light levels during experiments with contrasting intensities of white light and its eyes were most sensitive to green light (Loukashkin and Grant 1965), which is the wavelength transmitted maximally by the turbid, green coastal waters it inhabits (Hobson *et al* 1981). Bagarinao and Hunter (1983) noted that the action spectrum of *E. mordax* peaked at 530 nm, confirming the findings of Loukashkin and Grant (1965). Blaxter (1964; 1966; 1968a) demonstrated how the eyes of *Clupea harengus* became increasingly adapted to twilight vision as development progressed, although they never attained the sensitivity of the anchovy eye (Bagarinao and Hunter 1983). The eyes of several Black Sea

planktivores, including the anchovies and atherinids, are adapted for detecting rapidly moving prey in low light conditions (Protasov 1968). James (Chapter four) demonstrated that particulate feeding rates of *E. capensis* were similar in light and dark conditions, indicating that its eyes are also adapted for twilight vision.

The disparities existing between data sets probably do not reflect true differences in feeding periodicity, but are rather a reflection of environmental and biological influences and poor sampling strategies. Light has been pinpointed as an important factor, as it affects prey availability not only by restricting the ability of visual predators to locate their prey (Blaxter 1964; 1966; 1968; 1969; 1975; Woodhead 1966; Hunter 1968; Protasov 1968; Bagarinao and Hunter 1983), but also by influencing zooplankton and fish vertical migration patterns (Angelescu 1982; Angelescu and Anganuzzi 1981; Angel 1985; Hutchings 1985; Kerfoot 1985; Pillar in prep; Verheye and Hutchings 1988), thus affecting the non-visual filter feeders as well. Janssen and Brandt (1980) stated that adult alewives could only feed at night on large opaque prey, such as mysids, which provided an adequate silhouette for the predator to focus upon. Woodhead (1966) went as far as to state that the determination of diurnal feeding rhythms based solely on the examination of gut contents were of limited reliability since they need not indicate a true feeding rhythm but could simply reflect diurnal changes in prey accessibilty. The zooplankton prey migrate to the surface waters at night and are

thus most accessible to the planktivores at this time. However these fish are, in turn, also susceptible to predation and therefore may not be able to fully utilise their food resouce (Hobson 1968; Protasov 1968; Major 1977, 1978).

Spawning activity has also been shown to affect periodicity (Woodhead 1963, 1966). James (Chapter two) noted that spawning took precedence over feeding and delayed the peak feeding time of *E. capensis* by 6 hours on the Agulhas Bank spawning grounds compared to that observed on the West Coast recruitment area. Valdes *et al* (1987) also found that spawning and feeding were temporally separated in *E. capensis* in the spawning area, although they indicated that peak feeding activity preceded spawning. Similar spawning cycles have been documented for *Sardinops caerulea* and *E. mordax* (Ahlstrom 1959; Hunter and Macewicz 1980). Stage of development, fish length and season can also influence the extent and timing of diurnal activity cycles (reviewed in Woodhead 1966). Johnson (1939) and Furnestin (1953) observed that immature Passamaquoddy herring and *Sardinella aurita* remained shallower than the mature fish. It has been suggested such that differential activity cycles have high selective value since they reduce inter- and intra-specific competition to a minimum by partitioning resources (Aschoff 1964). Such shifts in activity and feeding cycles may explain some, especially intraspecific, variations observed in the available data (c.f. Chapter two and Valdes *et al* 1987).

Clupeids have long been recognised as opportunistic foragers (Schoener 1971; Koslow 1981; Angelescu 1982; Angelescu and Anganuzzi 1981; Chapter two) which will "snack" (Hopkins and Baird 1981) on suitable food as encountered, thereby making any periodicity very elastic and dependent upon environmental conditions. Therefore frequent and regular sampling is required to accurately define the cycle. Yet many studies have attempted to derive feeding cycles from inadequate samples. Some utilised only samples from commercial catches which were unevenly distributed over the 24 hour period (Davies 1957; de Mendiola 1971; King and Macleod 1976), while others had too few samples (Loukashkin 1970) or sampled only during restricted periods (Koslow 1981). A major problem has been that the determination of a diel feeding cycle was not a primary objective at the outset of many studies, which it must be considering the flexible, opportunistic foraging behaviour of these fish. Intensive sampling is also important in determining the diet of these fishes since prey accessibility and feeding behaviour vary during the cycle. Both Angelescu (1982) and James (Chapter two) showed that smaller particles increased in relative abundance in the diet during periods of low trophic activity when filtering was more prevalent and James (Chapter two) illustrated how the vertical migration of *Euphausia lucens* had a marked effect on the composition of the diet of *E. capensis* during a 24 hour period.

It is concluded that clupeids are generally twilight foragers, but that a variety of environmental and biological factors - many of which are unpredictable and not fully understood - can affect this periodicity. This conclusion is supported by the detailed studies available (Angelescu 1982; Chapter two).

DIET

There is little contention that the diets of particulate microphagists are composed almost entirely of selectively caught meso- and macro-zooplankton (Hardy 1924; Jesperson 1928; Battle *et al* 1936; Verheijen 1953; Blaxter and Holliday 1958; Rosenthal and Hempel 1970; De Silva 1973; Gibson and Ezzi 1985; Wallace-Fincham 1987). Similarly, the diets of true filter feeders are known to reflect the composition of the available plankton (Peck 1894; Ellison 1951; Darnell 1958; Bayliff 1963; June and Carlson 1971; Durbin and Durbin 1975), up to some threshold size, above which potential prey in the plankton are ignored or can escape the non- discriminatory filter feeders (Durbin and Durbin 1975). It is noteworthy that:

A) true filter feeders switch from selective particulate to non-selective filter feeding as development progresses (June and Carlson 1971; Durbin 1979; Govoni *et al* 1983), and

B) many filter feeders inhabit shallow coastal and estuarine waters which have a high detrital load and large biomasses of

active unicellular benthic primary producers, both of which are well represented in their diets; i.e. there is a tendency towards detritivory and iliophagy (Goode 1879; Hildebrand and Schroeder 1928; Darnell 1958; Bayliff 1963; June and Carlson 1971).

The controversy surrounds the diets of the intermediate microphagists, which have the ability to forage over three trophic levels, and the review will be restricted to these fishes.

Indian Coastal Waters

The diets of the Indian oil sardines, *Sardinella longiceps* and *S. gibbosa*, were originally considered to be composed primarily of zooplankton, especially copepods (Sundara Raj 1933; 1936). Later studies (Vijayaraghaven 1953; Nair 1960; Dhulkhed 1962; Bensam 1964; Kagwade 1964; Noble 1965; Longhurst 1971) indicated that these species were phytophagous, zooplankton being of only minor importance. Loukashkin (1970), on the other hand, classified *S. longiceps* and *S. gibbosa* as omnivorous but with a preference for zooplankton. Cushing (1978) supported Loukashkin's (1970) classification and criticised the subjective analytical techniques employed by several workers. Cushing (1978) argued that, since the sardines and sardinellas possess finer meshed gill rakers than other clupeids, they would inevitably collect the larger phytoplankters as they pursued crustaceans. He employed Kagwade's (1964) data to illustrate that if bulk rather than numbers were

considered zooplankton was 3-4 times more abundant than phytoplankton in the diet of *S. longiceps*.

Pacific

Studies on the diet of *Sardinops melanosticta*, have given rise to conflicting reports in the literature. Kishinouye (1907) noted an apparent switch in the diet from zooplankton when juvenile to phytoplankton when adult. Deriugin (1933), Koganovskaia (1934) and Koganovskii (1935) found a strong correlation between the composition of the plankton and the far eastern sardine'sdiet and concluded that the adults were indiscriminate filter feeders. Gail (1934) initially considered phytoplankton to be the preferred diet of this species but, after further investigation, reversed his conclusions and recognised zooplankton as its main food source (Gail 1936). Several other authors have emphasised the importance of zooplankton in the diet, stating that while phytoplankton may be important, it could only be considered as a "forced diet" in the absence of suitable zooplankton concentrations (Brodskii and Iankovskaia 1935; Brodskii 1936; Iankovskaia 1937).

Yamashita (1957a; b) studied the food of *S. melanosticta* and *Engraulis japonica* and observed a dietary switch similar to that found by Kishinouye (1907) that was accompanied by a rapid increase in the gut length : body length ratio which, he suggested, allowed the fish to utilise phytoplankton more efficiently. The

conclusion that *E. japonica* was phytophagous was not supported by other workers (Nakai *et al* 1955; Kubo 1961; Hayasi 1967) who found that zooplankton, especially copepods, were its principle food source. Nakai *et al* (1962) further noted that the size of prey consumed was positively correlated to fish length. Loukashkin (1970) stated that, while both these species displayed omnivory, they preferred animal food. Cushing (1978) reviewed Yamashita's (1957a; b) data and argued that zooplankton were numerically superior in the stomachs of both species and if weights were considered, then their diets were chiefly zooplanktonic.

Lewis (1929), on the basis of 207 stomach samples, concluded that the Pacific sardine, *Sardinops caerulea*, was primarily a phytophagous filter feeder. Parr (1930) using Lewis' (1929) data, contradicted his conclusion, stating that the sardine only sustained an interest in zooplankton, chiefly copepods, and collected phytoplankton inadvertently during the pursuit of their preferred prey. This conclusion was reversed by Hart and Wailes (1932) and Scofield (1934) who concluded that *S. caerulea* was phytophagous. Hand and Berner (1959) noted that the year Hart and Wailes sampled (1929) was marked by low oil yeilds, and Hart and Wailes did suggest that "red feed" (zooplankton) may be responsible for higher oil yields. Cushing (1978) reviewed the work of Hart and Wailes (1932) and stated that if the weight and volume instead of percent occurrence of each prey group were considered, then these fish were zoophagous. Radovich (1952) examined 42

samples before concluding that *S. caerulea* was zooplanktivorous, and a concurrent CalCOFI report (1952) sustained his conclusion, finding zooplankton in 100% but phytoplankton in only 75% of the adult stomachs examined. Hand and Berner (1959) conducted the most extensive investigation of the diet of the Pacific sardine and found that 89% of the diet was composed of crustacean remains, copepods being the most numerous items (74% of the contents). A strong correlation between the composition of the stomach contents and the plankton was noted, although the contents were occasionally composed entirely of one or two items. They concluded that *S. caerulea* was generally a non-selective omnivore with a preference for zooplankton, but recognised that this species had the ability to feed selectively. Hand and Berner (1959) identified 34 prey species in the stomachs examined, but this is unlikely these comprise the entire menu of the sardine. Loukashkin (1970) noted 96 prey items in 926 Northern anchovy, *Engraulis mordax*, stomachs, including the 34 found by Hand and Berner (1959). Since these two species cohabit, it is fair to assume that all 96 items would also be consumed by the sardine.

Loukashkin (1970) classified *E. mordax* as an omnivorous filter feeder with a preference for zooplankton, especially copepods and euphausiids (85%-90% of the total contents). He did, however, recognise the ability of this species to feed selectively, depending upon the size composition of the available plankton. Koslow (1981) also found that zooplankton comprised the bulk of

the diet of *E. mordax*. He demonstrated conclusively that *E. mordax* was an efficient selective feeder, capable not only of selecting for the largest prey available over a 100 fold range in prey size, but also of capturing 95-100% of that prey type as a school moved through a patch of plankton. This flexible feeding behaviour, which enables the fish to maximise their utilisation of the available food resources, is undoubtedly a cause of the conflicting reports concerning the diets of these fish in the literature.

Most studies state that the diet of the Peruvian anchoveta, *Engraulis ringens*, is composed mostly of phytoplankton (de Mendiola 1953; 1969; 1971). Whitledge (1978), on the basis of phytoplankton nitrogen requirements and estimates of "regenerated" versus "new" nitrogen in the Peruvian upwelling system, suggested that the anchoveta must consume a large portion of the primary production to maintain the excretion rates necessary to supply the ammonia required for primary production. Using samples from commercial catches and experimental fishing expeditions, de Mendiola (1969; 1971) found regional differences in the anchoveta's diet: phytoplankton dominated in the north (9°S, around Chimbote) while zooplankton was more important in the diet of southern fish (18°S, around Mollendo). The dominance of zooplankton in the diet of "southern anchoveta" has been noted by workers who studied *E. ringens* in Chilean waters (Schneider 1943; de Buen 1958). De Mendiola (1971) associated this north/south change in diet with meristic differences; the gut length:standard length ratio ranged

from 1.75:1 in the north (c.f. 1.71:1 from Harder [1958]) to 0.93:1 in the south. Similarly, the northern anchoveta had a greater number of gill rakers (87 on the first gill arch) than the southern fish (83 on the first arch). Tsukayama (1966) observed a similar north/south gradient in gill raker morphology. De Mendiola (1971) suggested the possibility of separate north Peru and south Peru/ north Chile stocks of *E. ringens* with different diets. The rationale being that the fewer gill rakers and shorter intestine of the southern anchoveta were indicative of a zooplankton diet, while the more numerous rakers and the longer gut of the northern fish, which comprised 92% of the commercial landings (Vasquez 1969), indicated that these fish, and hence the fishery, were dependent upon phytoplankton. This argument is widely accepted and it has been tacitly assumed for the purposes of global modelling of energy flow through upwelling systems that not only *E. ringens*, but all clupeids in these regions are herbivorous (Ryther 1969; Walsh 1975, 1980, 1981; Blaxter and Hunter 1982; Bergh *et al* 1985; Shannon and Field 1986).

Cushing (1978) disregarded the hypothesis of separate stocks with differing diets and instead suggested that the anchoveta north of Chimbote were more involved in spawning than feeding, while the southern fish, which were outside the spawning area, were actively feeding. Several authors have noted that clupeids reduce their feeding activity during the spawning season (Ramalho 1933; el Saby 1937; Lovern and Wood 1937; Hickling 1945), although the

TABLE 3. The daily ration required by *Engraulis capensis* (in ml/day). From Cushing (1978), using the data of da Mendiola (1971) and Jordan (1974).

FISH LENGTH mm	WEIGHT g	RATION (in ml/day) AS A % BODY WEIGHT/ DAY 1%	3%	5%
10.0	7.0	0.07	0.21	0.35
12.5	13.2	0.13	0.40	0.66
15.0	24.2	0.24	0.72	1.21

recent study of James (Chapter two) upon spawning *E. capensis* showed no such reduction. The difference in the diets between the northern and southern anchoveta could be due to changes in the feeding periodicity and vertical migration patterns in the spawning compared to the non-spawning fish, as noted for *Engraulis capensis* (Shelton and Hutchings 1982; Hampton *et al* 1985; Chapter two) which resulted in the spawning, but not the feeding fish being sampled. Using the data of de Mendiola (1971) and Jordan (1974), Cushing (1978) demonstrated that *E. ringens* could not obtain its daily ration from phytoplankton alone (Table 3). He calculated that the mean quantity of algae in a stomach was 0.065 ml, while a 12.5 cm anchoveta requiring a ration of 5% body weight per day needed 10 times this volume. Spawning fish may require even greater amounts; Hunter and Leong (1981) calculated that an average daily ration of copepods equivalent to 4-5% wet female weight was required to meet the annual costs of growth and spawning. Cushing (1978) stated that numerically, the quantities of phytoplankton in the guts of the northern anchoveta were similar to those found in the stomachs of zoophagous sardine-like fishes. He strengthened the argument further by observing that if most sardine-like fishes fed predominantly upon phytoplankton, they would have to swim very slowly (0.2 Body Lengths/sec, Yoshida 1955) to filter the phytoplankton from the water efficiently. This is an order of magnitude slower than *in situ* measurements of the foraging speed of anchovy (2-3 BL/s, Koslow 1981). These different interpretations of the same data confuse the issue of

the relative importance of zooplankton and phytoplankton in the diet of *E. ringens*. However, Cushing's (1978) review more recent studies (Koslow 1981; Angelescu 1982; Chapter two) provide convincing arguments for a primarily zoophagous diet for *E. ringens*.

Atlantic

The Atlantic sardine, *Sardina pilchardus*, has been extensively studied. Cépède (1907), Mangin (1912) and Fage (1920) all stated that metamorphosed sardine fed on "minute vegetable matter, peridinians being specially taken, with occaisional zooplankton" (quoted in Lebour 1921). Only Fage (1920) recognised that zooplankton could be important. However, more detailed studies concluded that this species was generally a selective zooplanktivore (Swithinbank and Bullen 1913; Lebour 1919, 1921, 1924), although juvenile fish sampled in estuaries contained fine mud, benthic diatoms and even small molluscs (Lebour 1921). The latter data are considered to be an artefact of the sampling location and serve to illustrate the variability in the diet of this species.

Desbrosses (1933) and Hickling (1945) found seasonal variations in the diet of *S. pilchardus*. Crustaceans, mainly copepods, were most abundant in the summer and phytoplankton, especially diatoms, predominated in the winter. Hickling (1945) considered copepods to be the most important component of the diet since they dominated during the period of greatest feeding activity (June - August). He

ranked the most important food items of *S. pilchardus*, based on frequency, as copepods; euphausiids; mysids; amphipods; crustacean larvae; diatoms and peridinians. On the basis of Hickling's (1945) study Loukashkin (1970) classified *S. pilchardus* as an omnivore which fed selectively upon zooplankton.

Limited work has been conducted upon the North African clupeids. The bonga, *Ethmalosa fimbriata*, closely resembles the Western Atlantic menhadens both anatomically and ecologically (Longhurst 1971), inhabiting the coastal waters and filter feeding upon the resident phytoplankton and microzooplankton populations (Bainbridge 1960, 1963). *Engraulis enchrasicolus*, which is present in the North African upwelling area feeds mainly upon zooplankton, as it does in other regions, although its diet may be more omnivorous in upwelling zones (Duka 1964; 1969; Mikhman and Tomanovich 1978).

Three *Sardinella* species occur in North African waters. *S. aurita* is only resident in the upwelling season between June and October, when it feeds mainly upon *Calanoides carinatus*, the dominant copepod during upwelling (Bainbridge 1960). *S. eba* and *S. cameronensis* have rather more catholic zooplankton diets (Longhurst 1971). Van Thielen (1977) studied aspects of the trophic ecology of *S. aurita* and *Anchoa guineensis* in the Ghanaian upwelling region and found that, although both species were zooplanktivorous, there appeared to be some degree of resource partitioning. *S. aurita* preferred copepods greater than 1.0mm long (confirming the

results of Bainbridge [1960]) while the diet of *A. guineensis* was composed almost entirely of copepods less than 0.5mm long. Van Thielen (1977) also noted that the diet of *S. aurita*, but not *A. guineensis*, contained significant quantities of sediment, which he considered an additional food source. Longhurst (1971) stated that most of the smaller tropical clupeids of the genera *Anchoa*, *Anchovia* and *Anchoviella* have unspecialised zooplankton diets.

The diet of the Argentinian anchovy, *Engraulis anchoita*, has caused some controversy. Angelescu and Fuster de Plaza (1962) and Fuster de Plaza (1964) found a switch from a phytoplankton to a zooplankton dominated diet between juveniles and adults. This is contrary to other dietary switches cited for clupeids (Kishinouye 1907; Yamashita 1957a,b; King and MacLeod 1976). De Ciechomski (1967a,b) reviewed the available data and concluded that *E. anchoita* was zoophagous in comparison to the "phytophagous" *E. ringens*, but that since this species appeared to be a nonselective feeder, the composition of its diet depended upon that of the plankton. In the most recent and comprehensive study, Angelescu (1981, 1982) and Angelescu and Anganuzzi (1981) defined *E. anchoita* as an opportunistic euriphage capable of foraging over three trophic levels which alternated between particulate and filter feeding, depending upon the size composition and distribution of the plankton and the diurnal cycle. Angelescu (1981) divided the environment of *E. anchoita* into different trophic habitats on the

TABLE 4. The seasonal occurence of zooplankton in the diet of *Sardinops ocellatus* collected in and around St. Helena Bay during 1953 - 1956. From Davies (1957).

MONTH	% ZOOPLANKTON	FULLNESS INDEX
January	62	6
Febuary	39	4
March	22	5
April	29	3
May	31	2
June	35	3
July	64	2
August	24	3
September	10	4
October	8	3
November	45	3

basis of the physical environment, plankton composition, biomass, productivity and accessibilty to the fish and concluded that the diet and feeding behaviour of this species varied with habitat and that the fish would migrate to the area of greatest trophic accessibility to maximise the efficiency of energy transfer. Angelescu (1982) and Angelescu and Anganuzzi (1981) identified the the major components of the diet as herbivorous copepods, cladocerans, euphausiids and fish eggs and larvae (especially anchovy) and stated that the phytoplankton, largely diatoms, in the diet should only be regarded as occasional food of limited importance.

Literature concerning the diets of South African clupeids are scarce. Wallace-Fincham (1987) determined that the round herring, *Etrumeus whiteheadi*, was a macrozooplanktivore with the bulk of the diet consisting of copepods, euphausiids and decapods. Davies (1957) carried out an extensive study of the diet of *Sardinops ocellatus*, examining 16 664 samples using the points method (Table 4) and concluded that this species was phytophagous, even though zooplankton comprised 1/3 of the contents, stating that zooplankton was only important "at times when the abundance of phytoplankton is diminished". Davies (1957) did, however, recognise that his data probably did not reflect the true importance of zooplankton in the diet of *S. ocellatus*, which he noted could "become a particulate feeder when necessary". Loukashkin (1970) considered *S. ocellatus* as omnivorous, regardless of any apparent preference for phytoplankton. Cushing (1978) reanalysed Davies'

TABLE 5. Seasonal occurence of zooplankton in the diets of A) *Engraulis capensis* and B) *Sardinops ocellatus* collected off the Namibian coast during 1971 - 1972.
From King and MacLeod (1976).

SEASON	% ZOOPLANKTON STANDARD LENGTH OF FISH EXAMINED mm			
	A	B	A	B
	20 - 80	20 - 100	80 - 153	100 - 268
	n = 240	508	169	348
Spring	83.6	84.8	29.3	20.0
Summer	90.3	89.8	35.9	26.8
Autumn	83.7	79.6	23.3	16.7
Winter	88.9	91.2	31.2	21.8

(1957) data, pointing out that if the proportions of phytoplankton and zooplankton were weighted by volume rather than by surface (as by the points method) then the proportion of zooplankton in the diet would be much greater than the 1/3 indicated by Davies (1957). Data from an ongoing study (James unpubl. data) suggest that zooplankton is considerably more important than Davies (1957) intimated.

Preliminary reports of the diet of *E. capensis* stated that this species was phytophagous (Robinson 1966; King and MacLeod 1976). The latter studied the diets of both the pilchard and the anchovy and observed an apparently dramatic switch in trophic habits from selective zoophagy to non-selective phytophagy at 80mm standard length in the anchovy and 100mm in the pilchard (Table 5), which they attributed to the completion of the development of the gill raker mechanisms at these lengths. Although King and MacLeod (1976) noted that the anchovy consumed relatively more zooplankton than the pilchard, they found no evidence of selective feeding behaviour in the adults of either species, stating that disparities in the diets were due to the differing porosities of the respective gill raker systems. However, the subjective analytical methods employed by King and MacLeod (1976) gave rise to doubt about the validity of their findings Chapter two). James (Chapters two and four) conducted field and laboratory studies to determine the diet, mode of acquisition and selective feeding behaviour of *E. capensis* and demonstrated that zooplankton, mainly calanoid copepods and

TABLE 6. A comparison of gill raker and intestine dimensions in A) *Cetengraulis mysticetus*, B) *Sardinops ocellatus* and C) *Engraulis capensis*. From Bayliff (1963) and King and MacLeod (1976).

MORPHOLOGICAL FEATURES	DIMENSIONS STANDARD LENGTHS mm								
	30 - 40			60 - 70			115 - 125		
	A	B	C	A	B	C	A	B	C
Arch Length mm	9.5	5.1	6.7	20.0	13.4	16.1	44.0	33.6	-
Raker Length mm	2.7	0.37	1.1	5.7	1.6	2.2	11.6	3.73	-
Raker Gap mm	0.22	-	-	0.26	0.19	0.24	0.37	0.27	0.42
Gut:Body Length Ratio	1.65	-	0.42*	3.53	0.96*	0.87*	8.5	1.47*	1.13*

* Data from present study.

euphausiids, provided the bulk of its diet and that the anchovy selected food items primarily on the basis of size. James (Chapter two) also observed patterns of feeding behaviour and periodicity similar to those described by Angelescu (1982) for *E. anchoita*.

If the gill rakers of *E. capensis* and *S. ocellatus* are compared to those of the true filter feeder, *Cetengraulis mysticetus*, whose gill rakers are well enough developed at 30mm standard length to filter out diatom chains (Bayliff 1963), it will be noted that the raker gap of the anchoveta is similar to that of the anchovy and considerably wider than that of the pilchard (Table 6). The data indicate that the gill rakers of *E. capensis* and *S. ocellatus* are sufficiently developed to trap diatom chains well below the standard lengths stipulated by King and MacLeod (1976). Therefore there is little justification for the relationship between gill raker morphology and the radical change in diet alluded to by these workers. Rather, there may be a gradual increase in the amount of phytoplankton occurring in the diets of these species which reflects the degree of development of the gill rakers, but that the absolute abundance of phytoplankton in the diet is dependent upon the frequency of filtering behaviour by the fish, which appears to be the secondary mode of intake and is itself dependent upon the availability of preferred food items (Chapters two and four). The trophic value of the ingested phytoplankton is also questionable (Chapter six).

TABLE 7. The diets of some sardine-like fishes related to the gut:body length ratio.

SPECIES	FEEDING BEHAVIOUR	DIET	GUT:BODY LENGTH	REFERENCE
Cetengraulis mysticetus	Filter	Planktonic and benthic diatoms	*1.65:1 (30mm) *3.53:1 (60mm) #8.50:1 (118mm)	Bayliff 1963, 1969
Brevoortia tyrannus	Filter	Mainly diatoms, some detritus and copepods	#4-5:1	Goode 1884, Durbin and Durbin 1975 Cushing 1978
Enraulis ringens	Mixed	North - diatoms South - copepods	#1.71-1.75:1 #0.93:1	Harder 1958, de Mendiola 1971
Sardinops ocellatus	Mixed	A) 2/3 phytoplankton B) 60-80% zooplankton	*0.96:1 (66mm) #1.47:1 (120mm)	A) Davies 1957 B) Present study
Engraulis capensis	Mixed	A) 60% phytoplankton B) 90% zooplankton	*0.42:1 (39mm) *0.87:1 (62mm) #1.13:1 (116mm)	A) King and MacLeod 1976 B) Present study and Chapter two.
Sardinops melanosticta	Mixed	80% zooplankton	*±0.80:1 (60mm) #±1.25:1 (122mm)	Brodskii and Iankovskaia 1935 Yamashita 1957a,b.
Engraulis japonicus	Mixed	80% zooplankton	*±0.80:1 (58mm) #±1.00:1 (108mm)	Yamashita 1957a,b, Shen 1969
Engraulis mordax	Mixed	86% zooplankton	#1.01:1	Loukashkin 1970
Sardinops caerulea	Mixed	89% zooplankton		Hand and Berner 1959
Engraulis anchoita	Mixed	95% zooplankton	*0.40:1 (30mm) #±0.80:1 (±90mm)	de Ciechomski 1967, 1974, Angelescu 1982
Clupea harengus	Particulate (May filter)	100% zooplankton	#±0.50:1	Cushing 1978, Gibson and Ezzi 1985, Nikolsky *et al* 1963
Etrumeus whiteheadi	Particulate	100% zooplankton	#0.66:1	Wallace-Fincham 1987, James unpubl. data
Etrumeus micropus	Particulate	100% zooplankton	#±0.50:1	Yamashita 1957a,b.

* Juvenile
\# Adult

The morphology of the alimentary canal appears to reflect the degree of specialisation towards microphagy, i.e. towards true non-selective filter feeding with a diet dependent upon the relative abundance of phytoplankton and zooplankton in the water column (Table 7). True phytophagous species possess long intestines with many pyloric caecae (up to 400 in the menhadens compared to only 20 in the herring), and the cardiac stomach is modified into a muscular gizzard with no absorptive function but capable of crushing diatom frustules and exposing the cell contents for digestion (Bayliff 1963, 1969; Nikolsky *et al* 1963; June and Carlson 1971). Sargent *et al* (1979) suggested that caecae were evolved for prolonged storage to ensure complete digestion of food. The intermediate microphagists which abound in upwelling areas do not possess such alimentary tracts, and as such are not as well eqipped to process a phytoplankton diet as some studies would suggest. Some workers regard any specialisation of the alimentary tract as unnecessary to utilise phytoplankton, believing that the "delicate" frustules would be destroyed by the peristaltic action of the gut and consider the only necessary specialisation to be the development of an effective gill raker mechanism (Ryther 1969; Longhurst 1971; King and MacLeod 1976). However, Radovich (1952) observed diatoms passing through the gut of *S. caerulea* unharmed, indicating that these fish were unable to fully utilise this food source. Crustacea, on the other hand, are readily digested by clupeids (Angelescu 1981; Durbin and Durbin 1981; Seiderer *et al*; Chapter two). Seiderer *et al* (1987) demonst-

rated that *E. capensis* possessed a chitinase enzyme capable of disrupting the exoskeletons of ingested crustaceans. Even in specialised filter feeders that depend heavily upon phytoplankton for food, the assimilation efficiency for zooplankton is greater than that for phytoplankton (Durbin and Durbin 1981).

CONCLUDING REMARKS

Intermediate microphagous clupeids display a high degree of opportunism in fulfilling their dietary requirements - they are energy maximisers, capable of alternating their feeding stategies to efficiently utilise the available trophic spectrum. The multitude of studies, the majority of which are inadequate (Cushing 1978; Chapter two) indicate that these fishes are primarily zooplanktivorous. The morphology of the alimentary tracts of these microphagists are intermediate between the filter and the particulate feeders, indicating that phytoplankton is utilised to some degree. However, the extent of utilisation depends upon the relative abundances of the preferred crustacean prey, the diurnal cycle, the state of shoaling and the degree of development of the gill raker system. Pilchards and sardines tend to consume more smaller particles than anchovies and they are morphologically better suited to capture and process this diet (June and Carlson 1971; King and MacLeod 1976; Cushing 1978; Blaxter and Hunter 1982), but they do have the ability to feed selectively (Hand and

Berner 1959; van Thielen 1977; Table 7).

The flexible and oppurtunistic feeding habits of these fishes have caused some of the misconceptions concerning their diets - when considered *en masse* the most striking features of most studies are;

A) the great variability in the composition of the diet of a species, both within and between studies, and

B) the unreliability of straight forward gut content analyses as a method of determining the trophic habits of these fishes.

Indeed, most of the confusion results from inadequate sampling and analytical techniques. Many investigations examined samples from restricted portions of the diurnal cycle, which is unacceptable considering the changes in feeding activity and behaviour observed by Angelescu (1982) and James (Chapter two) during 24 hour cycles. The analytical techniques employed during most studies were subjective and tended to bias the results in favour of the smaller, numerically superior phytoplankton while underestimating the importance of the larger zooplankton (Chapter two). The range in size of food items of these fishes (10-6mm for diatoms to 10-20mm for mesozooplankton, Chapter two) makes it essential that any analytical method employed assess the importance of dietary components by mass or bulk and not by numbers, since it is the amount and not the frequency of an item which is trophically important. Furthermore, an estimate of dietary value, e.g. carbon content (Chapter two), assists in determining the true importance

of a food type.

However, examining only the ingested food cannot assess the real importance of individual components in the diet, since each sample is nothing more than a single "snapshot" of the diet, being dependent upon the relative availability of the various prey types in the environment and, as such, providing limited information and having no predictive value concerning the factors affecting the acquisition of food. This fact is clearly illustrated by the of conflicting reports concerning the diets of these fishes in the literature. The ambient plankton community must be sampled simultaneously with the stomach contents so that the diet may be assessed in relation to the available food, allowing the underlying trophic processes to be understood and quantified (Koslow 1981; Chapter two). The more recent and thorough studies of Koslow (1981), Angelescu (1982) and James (Chapter two) investigated the trophic ecology of intermediate micophagists by assessing the selective feeding behaviour of these fishes. All three arrived at similar conclusions: these fish obtained the bulk of their diet through size-selective particulate feeding upon zooplankton, especially herbivorous copepods. Filter feeding upon phytoplankton was of secondary importance.

Laboratory observations and work investigating the selective feeding behaviour and grazing rates of these fishes upon different food types provides more detailed information than is possible from

field studies (Leong and O'Connell 1969; O'Connell 1972; O'Connell and Zweifel 1972; Durbin and Durbin 1975; Gibson and Ezzi 1985; Chapter four) and furthers our understanding of the processes governing feeding in intermediate microphagists. After determining the major dietary components and the basis of their selection, the logical progression would be to assess their energetic importance. This is the "bottom line" concerning the trophic ecology of a species, since it is the contribution that a food type makes towards the growth and reproductive requirements of an organism that is truely important. This involves detailed laboratory experiments assessing the energy expenditure of obtaining a food type using the different feeding strategies versus the energy gain and the ability of the fish to utilise a food type efficiently. There are few such studies on pelagic fish (Durbin and Durbin 1975, 1981,1983; Durbin *et al* 1981) and none for intermediate microphagists. This combined field and laboratory approach is the only feasible method of definitively determining the relative importance of phytoplankton and zooplankton in the diet of intermediate microphagous clupeids.

Clearly it is not the fact that these fishes can feed directly upon the primary producers that has resulted in their huge abundance in upwelling areas. Rather their feeding behaviour is flexible enough to allow them to efficiently utilise the entire range of plankton that may occur in these unstable regions at any time.

CHAPTER TWO

Feeding ecology, diet and field based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist.

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FEEDING ECOLOGY, DIET AND FIELD-BASED STUDIES ON FEEDING SELECTIVITY OF THE CAPE ANCHOVY *ENGRAULIS CAPENSIS* GILCHRIST

*A. G. JAMES**

Samples collected during four cruises on board R.S. *Africana* were used to study the trophic ecology and feeding behaviour of *Engraulis capensis* in the southern Benguela region. Previous work had indicated that this species was a non-selective filter-feeding omnivore, diatoms comprising the bulk of the diet. The results of the present study reveal that anchovies selectively feed on mesozooplankton, especially calanoid copepods and euphausiids. Investigation of the feeding behaviour of the species indicates that raptorial feeding is dominant over filter-feeding and that prey appears to be selected primarily on the basis of size.

Die trofiese ekologie en vreetgewoontes van *Engraulis capensis* in die suidelike Benguelastreek is ondersoek uit monsters van vier vaarte met die N.S. *Africana*. Vorige werk het aangedui dat hierdie spesie 'n nie-selektiewe filtervretende omnivoor is en dat die dieet oorwegend uit diatome bestaan. Volgens die resultate van die huidige ondersoek vreet ansjovis selektief mesosoöplankton - veral kalanoïede kopepodes en eufausiides. Ondersoek van die spesie se vreetgewoontes dui daarop dat grypvoeding oorheers oor filtervoeding en dat prooi primêr volgens grootte uitgesoek word.

Anchovy *Engraulis capensis* is the major component of the South African and Namibian (South West African) purse-seine fisheries and is also a key prey species for such predators as tuna *Thunnus* spp., snoek *Thyrsites atun*, seabirds and fur seals *Arctocephalus pusillus pusillus*. Little information is available on trophic ecology or feeding behaviour of anchovy. Robinson (1966) made limited observations on its diet in South-Western Cape waters and concluded that it displayed a "preference" for phytoplankton. King and Macleod (1976) conducted a preliminary investigation off Namibia and concluded that adult anchovies were herbivorous, switching from selective carnivory as juveniles, to non-selective, filter-feeding phytophagy as adults. They found no evidence of selective feeding behaviour by the adults. These findings agreed with the theories prevalent at the time that large populations of clupeoids in upwelling areas were sustained by their ability to feed directly on primary producers (Ryther 1969, Longhurst 1971).

Close examination of the sampling strategies and analytical methods employed by King and Macleod (1976) gave rise to doubt about the validity of their conclusions. The inclusion of intestinal contents in their analysis, the subjective estimation of volume of food types and the use of frequency-of-occurrence data to illustrate the importance of food items have been strongly criticized as inadequate processing techniques or measures of dietary importance (Doud 1974 as cited by Gannon 1976, Berg 1979, Hyslop 1980). Any detailed analysis of the trophic ecology of a planktivore should include not only an objective assessment of the gut contents but also a consideration of the potential food available in the plankton (Keast 1978, Berg op. cit., Clarke 1980, Hyslop op. cit. and references therein). A review of the literature (Cushing 1978, James 1984) and a comparison between the findings of King and Macleod (op. cit.) and those of more recent and detailed work (Angelescu and Anganuzzi 1981, Koslow 1981, Angelescu 1982) demonstrated that the findings of King and Macleod were inconsistent with the trends evident in modern literature. In addition, laboratory work indicated that *E. capensis* displayed selective feeding behaviour (James in prep.).

A detailed study of the diet and the feeding behaviour of Cape anchovy was therefore initiated to:

(i) investigate the feeding periodicity of *E. capensis*;
(ii) determine quantitatively the major components of the diet;
(iii) determine the modes of acquisition of the food and to investigate any change in feeding behaviour associated with increasing age;
(iv) investigate what criteria, if any, anchovies utilize to select food items from the plankton.

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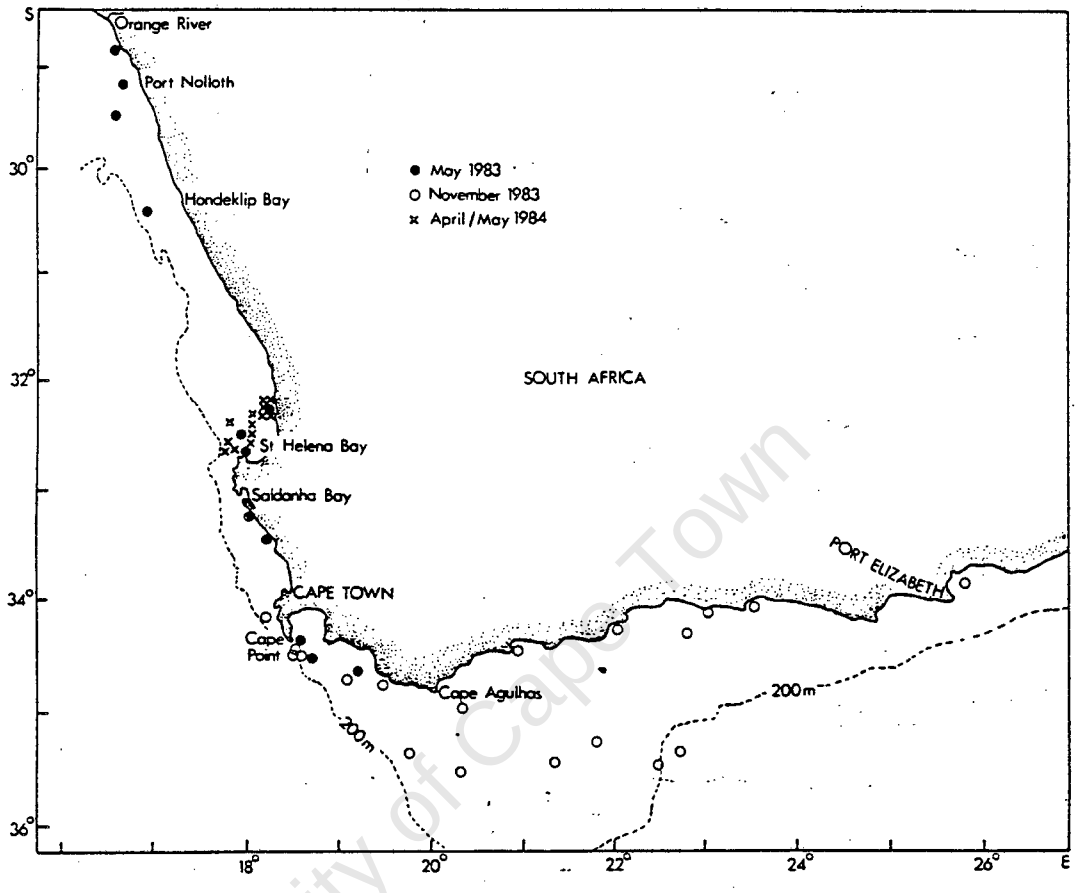

Fig. 1: Trawl and plankton sample positions around the coastline of South Africa

METHODS AND MATERIALS

Sampling was conducted from R.S. *Africana* during May 1983 and April and May 1984 off the west coast, and during November 1983 off the south coast of South Africa (Fig. 1). Fish were caught by a midwater trawl lined in the codend with 12-mm mesh. Concurrent zooplankton, microplankton and phytoplankton samples and hydrographic data were collected above, below and within the depth range occupied by the shoal at each trawl station by means of a multiple opening/closing rectangular midwater trawl (5 nets with a 1-m^2 mouth opening and 200-μm mesh) and a rosette sampler equipped with a C.T.D. A random sample of fish from each trawl was immediately blast-frozen for gut-content analysis and further samples were measured and examined to establish gonad state. All plankton samples were preserved in 10-per-cent buffered formalin.

In the laboratory, the trawl samples were thawed in a 10-per-cent formalin solution and separated into 10-mm size classes. Each fish was checked for signs of regurgitation of the stomach contents and rejected if the stomach walls were slack, if the stomach contained only a watery fluid or if there were digested food particles in the oesophagus and/or gills. The alimentary tracts from the oesophagus to the anus of 5–20 fish of each size class were then removed and stored, for later analysis in 4-per-cent neutral formalin prepared according to Steedman (1976). Equal numbers of fish were examined of each size class from each trawl. The gut contents to be examined were defined as that material contained in the pyloric and cardiac stomachs of the fish — the contents of the oesophagus and intestines were discarded to reduce bias caused by different rates of digestion, gut passage times (Fischer 1967, Doud 1974 as cited by

Table I: Relationships employed to calculate dry and wet weights and carbon and nitrogen contents of the food categories and plankton. All length : dry weight regressions were determined during the present study

Food category	Length : dry weight regression*	Conversion of dry to wet weight	Carbon as dry weight (%)	Nitrogen as dry weight (%)	Reference
Copepods	$a = 19{,}425b^{2.59}$	7,143	35–48	8,2–11,2	Beers 1966
Cladocera	$a = 3{,}946c^{2.436}$	7,143	35–48	8,2–11,2	Beers 1966
Nauplii	$a = 80{,}627c^{4.271}$	7,143	35–48	8,2–11,2	Beers 1966
Eggs	Volume calculated (sphere)	3,300	48,0	11,2	Beers 1966
Bivalve veliger larvae	$a = 47{,}386c^{3.663}$	7,092	31,25	8,32	Holland 1978
Gastropods	Volume calculated (cone)	7,092	31,25	8,32	Holland 1978
Chaetognaths	$a = 0{,}015c^{2.668}$	14,925	22–34	6,3– 9,4	Beers 1966
Euphausiids	$a = 0{,}0019c^{3.19}$	6,154	35–43	9,4–10,5	Beers 1966
Amphipods	$a = 0{,}005c^{2.311}$	3,636	26–48	4,4– 8,2	Omori 1969
Cyprid larvae	Individual weights measured	4,329	39,97	7,53	Lucas 1979
Zoea	Individual weights measured	7,143	41,5	9,7	Beers 1966
Anchovy	$a = 0{,}0001d^{3.582}$				

Parameter	Volume to carbon and carbon to nitrogen conversions	Reference
Diatoms (volume to carbon)	$\log_{10}C = 0{,}76\ (\log_{10}\text{volume}) - 0{,}352$	Parsons *et al.* 1984
Other phytoplankton (volume to carbon)	$\log_{10}C = 0{,}94\ (\log_{10}\text{volume}) - 0{,}60$	
C : N ratio of diatoms and other phytoplankton	6 : 1	
Tintinnids (volume to carbon)	$Cpg \times 10^3 = 0{,}445 = 0{,}053$ (lorica volume)	Verity and Langdon 1984
Tintinnids C : N	$Npg \times 10^3 = 0{,}068 + 0{,}24$ (carbon $pg \times 10^3$)	

Food category	Geometric shape	Reference
Tintinnids	Cone	Pitcher pers. comm.
Diatoms		
Thalassiosira	Cylinder	Edler 1979
Chaetoceros	Cylinder	Pitcher pers. comm.
Skeletonema	Cylinder	Edler 1979
Nitzschia	½ parallelepiped	Mitchell-Innes pers. comm.
Thalassiothrix	½ parallelepiped	Mitchell-Innes pers. comm.
Pleurosigma	½ parallelepiped	Pitcher pers. comm.
Rhizosolenia	Cylinder	Pitcher pers. comm.
Centrics (unidentified)	Cylinder	Mitchell-Innes pers. comm.
Pennates (unidentified)	Parallelepiped	Pitcher pers. comm.
Asteromphalus	Cylinder	Pitcher pers. comm.
Coscinodiscus	Cylinder	Pitcher pers. comm.
Leptocylindrus	Cylinder	Pitcher pers. comm.
Melosira	Cylinder	Pitcher pers. comm.
Lauderia	Cylinder	Pitcher pers. comm.
Plagiogramma	Cylinder	Pitcher pers. comm.
Hemiaulus	Cylinder	Pitcher pers. comm.
Asterionella	Cone	Pitcher pers. comm.
Biddulphia	Cylinder	Pitcher pers. comm.
Navicula	½ parallelepiped	Pitcher pers. comm.
Dinoflagellates		
Prorocentrum	Ellipsoid, circular cross-section	Edler 1979
Dinophysis	Ellipsoid, circular cross-section	Edler 1979
Peridinium 1	Sphere	Pitcher pers. comm.
Peridinium 2	3 × cone	Pitcher pers. comm.
Ceratium	3 × cone	Pitcher pers. comm.
Blue-green algae	Sphere	Mitchell-Innes pers. comm.

* *a* Dry weight (μg); *b* Prosome length (mm); *c* Total length (mm); *d* Standard length (mm)

Gannon 1976, Berg 1979, Hyslop 1980) and codend feeding (Judkins and Fleminger 1972, Hopkins and Baird 1975, Lancraft and Robison 1980, Nicol 1984).

The contents of all the guts from fish in a single size class were pooled, after preliminary examination of individual stomachs showed no statistically significant difference between the contents of fish of a similar size from the same trawl ($F = 0{,}39, p < 0{,}05$).

The sample was examined at 40× magnification and items with a greatest dimension exceeding 100 μm were removed, identified and measured. The remains of the sample were then made up to 50 m*l* and 3–5 2-m*l* subsamples were stained with Rose Bengal and examined at 400× magnification according to the enumeration technique of Utermöhl as described in Hasle (1978). The zooplankton was identified into major plankton groups and the phytoplankton to genera and cell type (Table I). The dimensions of all intact items were measured with an ocular micrometer, phyto- and microzooplankton to 1 μm and the larger zooplankters to the nearest 10 μm. Unmeasurable damaged items were assumed to occur at the same frequency as the undamaged portion. Chaetognaths, which are rapidly digested leaving only their bristles, were assumed to have the same size distribution as in the plankton samples, because there was insufficient material suitable to construct a regression of bristle length to total length. The sample was then reconstituted and dried at 60° C for 24 h, and weighed to 0,0001 g to measure stomach fullness. The food type, size and shape data were used to calculate the dry and wet weights and carbon and nitrogen contents of the food types from the relationships in Table I. Phytoplankton carbon values were converted to dry weight from the value quoted by Cushing *et al.* (1958).

Hureau's (1969) index of repletion (fullness index, FI) was used to determine times of peak feeding activity during 24-h feeding cycles:

$$FI = \frac{\text{Mean dry weight of gut contents}}{\text{Dry weight of fish}} \times 100\% .$$

The trawl data from the 24-h feeding studies of April and May 1984 were separated into four collection periods — dawn, midday, dusk and midnight. The data from the May and November 1983 cruises were analysed on the basis of stomach fullness rather than time of day because of the paucity of the data.

Zooplankters were counted from 1/16, 1/32 or 1/64 of the multiple opening/closing net samples, the microplankton samples were processed according to Armstrong (1987) and 3 × 25 m*l* aliquots of each phytoplankton sample were enumerated. The samples were categorized and processed in a similar manner to that applied to the gut contents to obtain dry and wet weights and carbon and nitrogen contents of the food per cubic metre of water sampled.

There are many selectivity indices available in the literature (Shorigin 1939, Ivlev 1961, Drenner and de Noyelles 1982, Lechowicz 1982, and others reviewed in Pearre 1986), all of which assess selective behaviour by comparison of the number or percentage composition of the gut contents to that of the plankton. However, preliminary tests demonstrated that assessment by number was unsatisfactory due to the preponderance of minute food items and the great range in size of the food items (10^{-6}–10^{-5} mm for diatoms to 10 mm for zooplankton). Therefore, bulk was employed to investigate selectivity.

Apparent Search Volumes (ASV), defined as the minimum volume of water searched by a fish to obtain the weight of a particular item found in the gut and with larger ASVs indicating greater preference for a prey type, were calculated to investigate the feeding selectivity of *E. capensis*:

$$ASV = \frac{\left\{ \dfrac{\text{Mean carbon weight of item in the gut}}{\text{Carbon weight of item per cubic metre in plankton}} \right\}}{\text{Mean dry weight of fish}}$$

The ASV was developed from the method described by Clarke (1980), whose ASV compared the number of items in the gut with the number of items in the plankton. ASV has units of m^3-g fish weight^{-1} as opposed to Clarke's ASV units of $m^3 \cdot fish^{-1}$ because the bulk of the item in the guts was standardized against the weight of the fish to allow direct comparison between different size classes of predator. Pearre (1986), reviewing several selection indices, noted that Clarke's (1980) ASV was a useful approach, despite not having a fixed value, e.g. 0 or 1 for zero selection, as found in many other indices (Shorigin 1939, Ivlev 1961, Lechowicz 1982, and others cited in Pearre op. cit.). As with Clarke's (1980) ASV, the present method assumes that the fish have not depleted the available food resources in the area prior to sampling.

RESULTS

Feeding periodicity

WEST COAST, MAY 1983, APRIL AND MAY 1984

The May 1983 data are a composite of 12 *ad hoc* trawls collected over a twenty-five day period. The

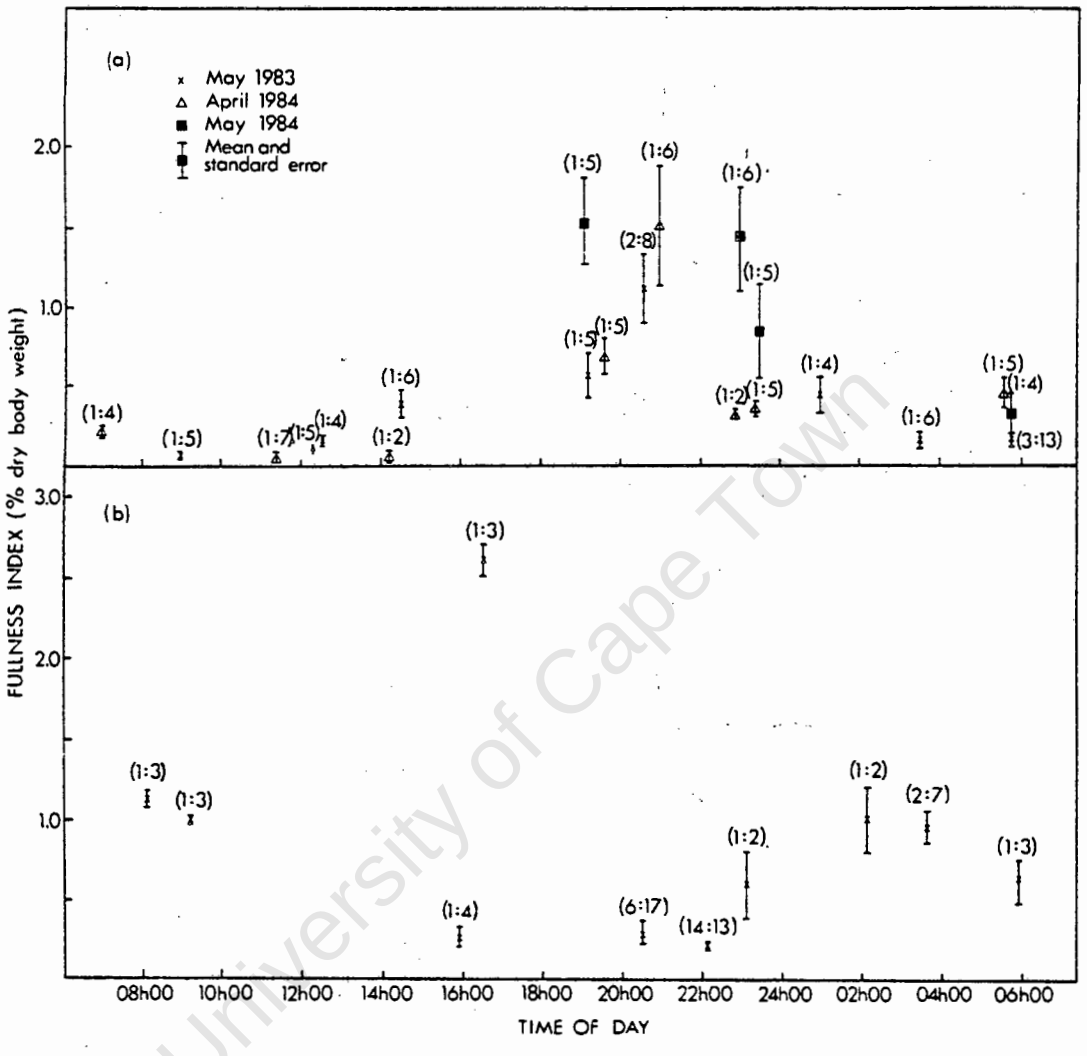

Fig. 2: Feeding periodicity during (a) the West Coast cruises (May 1983, April and May 1984) and (b) the South Coast cruises. Trawls have been grouped on an hourly basis. Values in parenthesis indicate the number of trawls and size classes

April and May data consist of samples collected during three (April 1984) and two (May 1984) 24-h feeding studies conducted in St Helena Bay.

The stomach fullness data indicate that *E. capensis* displays a marked synchronicity in feeding, a peak occurring between dusk and midnight when the stomachs contain up to 1,5 per cent of the dry body mass (Fig. 2a). The period of lowest fullness was between dawn and dusk (mean fullness 0,18 per cent of dry body mass).

The standard error around the mean stomach fullness values (Fig. 2a) are relatively smaller during periods of low fullness, indicating that the feeding rates of all size classes of fish are uniformly low. The increased variation during periods of greater fullness suggest that not all fish size classes feed at uniform rates, although the data from the pilot study indicate that the variation between fish in the same size class is small ($F = 0{,}39$, $p < 0{,}05$). These differences are probably related to the size spectrum of the available prey relative to fish size and to the feeding mode (raptorial or filter-feeding) employed. Individual acts of opportunistic feeding or "snacking" (Hopkins and Baird 1981) between major feeding bouts appeared

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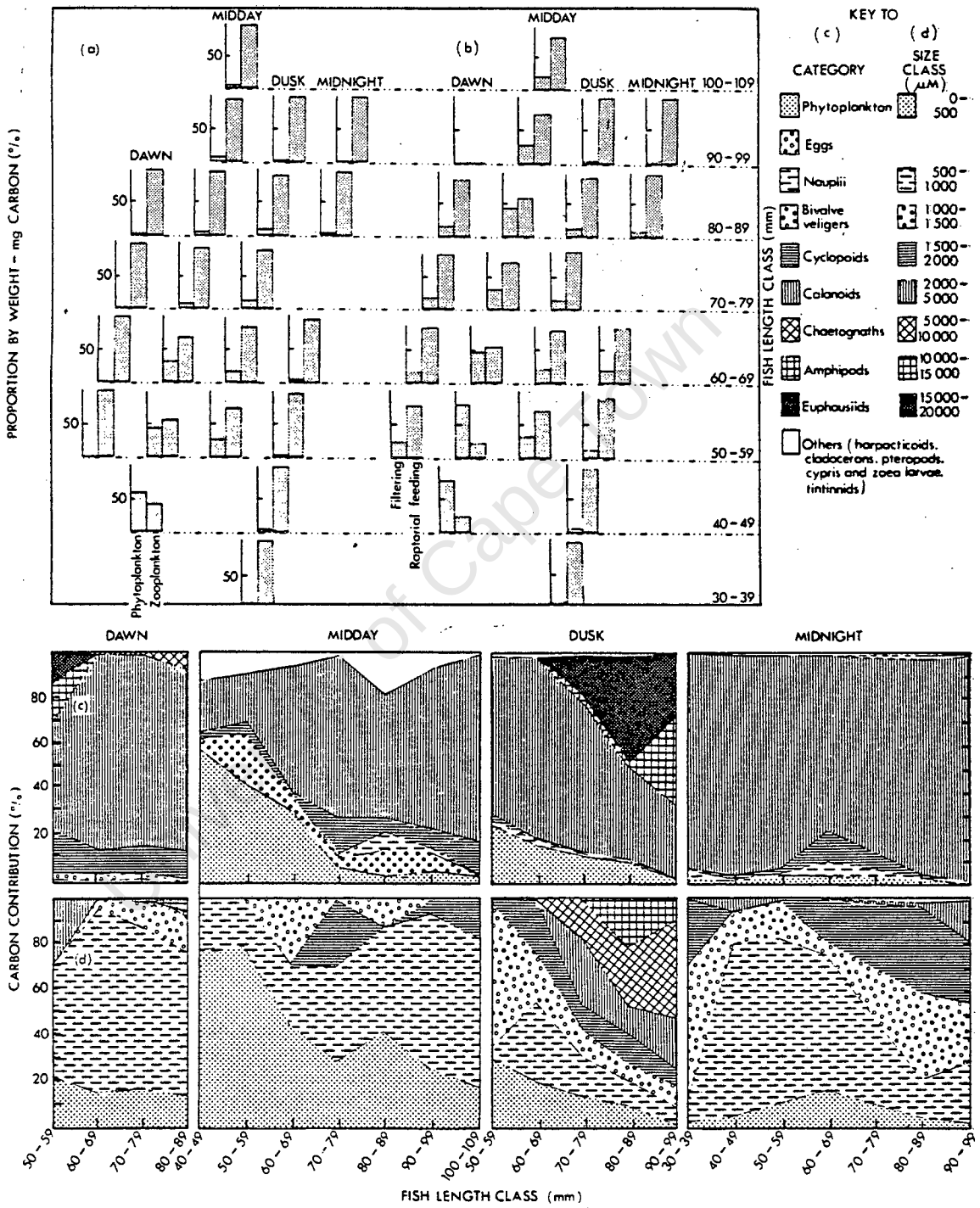

Fig. 3: (a) Proportions of zooplankton and phytoplankton in the stomachs; (b) proportions of stomach contents acquired by filter- and raptorial feeding; (c) prey composition in the diet; (d) prey size spectrum in the diet, all of *E. capensis* caught in St Helena Bay during April 1984

to be insignificant, although *E. capensis* feeds at non-zero levels throughout the day.

SOUTH COAST, NOVEMBER 1983

The data from the November 1983 cruise, consisting of 19 trawls of which 15 were at night, are scant and patchily distributed over the 24-h time-base (Fig. 2b). Because of the paucity of the data, no effort was made to divide the fish into prespawning, spawning and postspawning categories. A diel cycle is evident, but there is an approximately 6-h phase-shift compared to the West Coast data (Figs 2a, b). During this cruise the stomachs were emptiest between 12h00 and 22h00 (0,261 per cent of dry body mass), after which there was a sharp increase to a peak at 02h00 (1,0 per cent of dry body mass), which was maintained until mid-morning.

The major feeding period on the South Coast was considerably longer (23h00–10h00) than on the West Coast (19h00–24h00). The stomachs of fish from the South Coast were generally fuller during off-peak periods than those on the West Coast, suggesting more opportunistic feeding between major feeding bouts. The greatest stomach fullness values were recorded in the afternoon on the extreme eastern boundary of the Agulhas Bank (2,61 per cent of dry body mass, Station 124–04A, Fig. 1) and were not synchronous with the major feeding bout. This type of opportunistic feeding illustrates the optimal foraging strategy common among planktivorous fish (Schoener 1971, Werner and Hall 1974, Angelescu and Anganuzzi 1981, Koslow 1981, Angelescu 1982).

Diet composition

WEST COAST, APRIL 1984

Zooplankton comprised the bulk of the diet of *E. capensis* during all phases of the feeding cycle (Fig. 3a). Calanoid copepods between 0,5 and 2,0 mm were the dominant items (Figs 3c, d). During the peak feeding period, larger prey (amphipods and euphausiids) were prominent in the stomachs of larger fish (Fig. 3c - dusk). At midday many smaller food types, e.g. crustacean eggs, nauplii and cyclopoid copepods, and occasionally small quantities of silt and the benthic diatom *Triceratium* appeared in the diet. The contribution of phytoplankton to the dietary carbon was greatest in the smaller fish (Fig. 3a, c) at midday but decreased in importance with increasing fish size. *Rhizosolenia setigera* (cell length 0,37 mm) made up the bulk of the phytoplankton in the stomachs.

Experimental data (James in prep.) have demonstrated that juvenile and adult *E. capensis* filter-feed on particles $< 0,5$ mm maximum dimension and selectively feed raptorially on items $> 0,7$ mm maximum dimension. Particles between 0,5 and 0,7 mm fall into a "grey area", in which predator size interacts with prey size and concentration to modify feeding behaviour. Observations of feeding behaviour show that there is a threshold concentration of particles required to initiate filter-feeding, but none discernible for raptorial feeding. The fish will feed raptorially even if the prey are introduced to the tank individually. Furthermore, if small prey which elicit filtering and larger items which elicit raptorial feeding are presented to the fish simultaneously, then raptorial feeding is dominant, actually supressing filtering activity even if the biomass of the smaller particles is greater (James op. cit.). These findings are similar to those recorded for other clupeoids (Leong and O'Connell 1969, O'Connell 1972, Hunter and Dorr 1982, Gibson and Ezzi 1985). For the purposes of the present analysis, it has been assumed that prey items less than 0,5 mm were acquired by filtering and those greater by raptorial feeding. This division is simplistic for small fish (< 60 mm), which do not possess a well developed gill-raker mechanism (King and Macleod 1976) and which direct their particulate feeding activity towards smaller items. It must therefore be borne in mind that this directed feeding will inflate the importance of filter-feeding in smaller fish.

The probable mode of acquisition of the stomach contents is illustrated in Figures 3b and 3d. Raptorial feeding on items of $> 0,5$ mm was dominant, especially during periods of elevated trophic activity. Filter-feeding on prey $< 0,5$ mm declined with increasing fish length. The large contribution by phytoplankton to the diets of small fish during this cruise was probably a result of directed raptorial feeding on cells of *R. setigera* and *Pleurosigma* spp. (cell length 0,30 mm). Filter-feeding was most evident at dawn and especially midday, the periods of lowest feeding activity.

During the period of most intense feeding (dusk), there was a clear trend of increasing prey size with increasing fish length (Fig. 3d). This trend was evident, though less obvious, at intermediate feeding levels (midnight), and was not apparent during periods of low trophic activity (dawn and midday). The size range of prey in the stomachs similarly declined with decreasing feeding activity. These changes are due to the prevalence of non-selective filter-feeding during periods of low trophic activity.

WEST COAST, MAY 1984

A violent westerly storm occurred between the April and May cruises which advected large numbers

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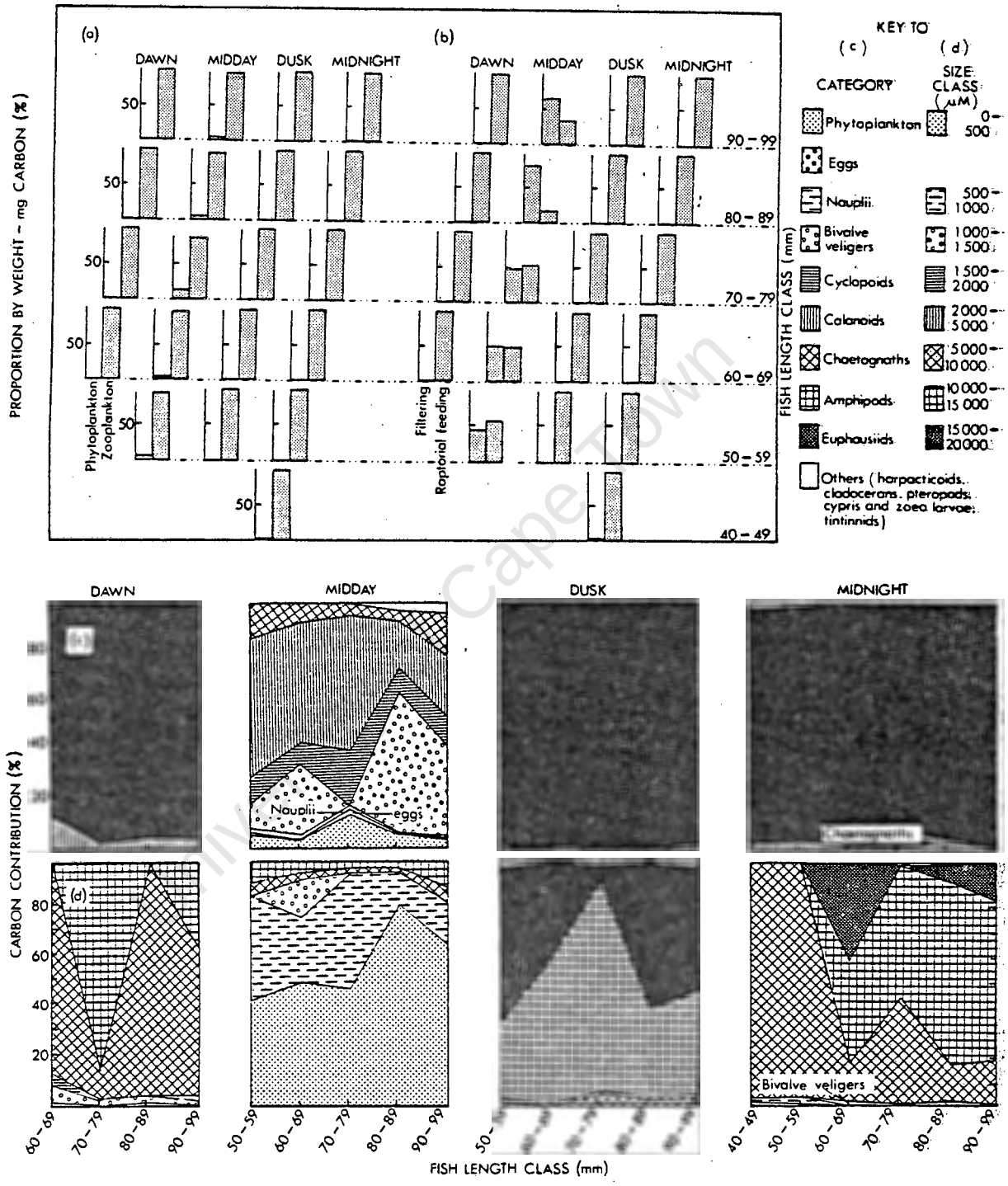

Fig. 4: (a) Proportions of zooplankton and photoplankton in the stomachs; (b) proportions of stomach contents acquired by filter- and raptorial feeding; (c) prey composition in the diet; (d) prey size spectrum in the diet, all of *E. capensis* caught in St Helena Bay during May 1984

of euphausiids into St Helena Bay from offshore. This advection dramatically increased the size spectrum of prey available to anchovies during the May cruise as compared with April.

Zooplankton was again the major component of the stomach contents, contributing almost all the dietary carbon during all phases of the feeding cycle except midday, when phytoplankton provided 2–10 per cent of the total (Fig. 4a). Euphausiids 5–20 mm long dominated the stomach contents of all size classes of anchovy during periods of elevated trophic activity, with calanoid copepods making up the balance (Figs 4c, d). Euphausiids were absent from the diet at midday, when the bulk of the carbon present originated from phytoplankton, bivalve veliger larvae, cyclopoid and calanoid copepods. Verheye (in prep.) observed that euphausiids were abundant in the water column throughout the night but absent during the day, when they had presumably migrated to the bottom layers (Pillar 1982). Small quantities of mud, *Triceratium* and an unidentified dipteran wing were occasionally found in the midday samples.

Raptorial feeding was the prevalent mode of acquisition of prey during active foraging (dusk to dawn — Fig. 4b). There was a marked change in feeding behaviour at midday, when filtering was the dominant mode which could be attributed to the absence of euphausiids. The switch in feeding behaviour is similar to that described for *E. anchoita* by Angelescu (1982). The bulk of the food acquired by filtering consisted of bivalve veliger larvae (Fig. 4c). There was a sharp increase in the proportion of food acquired by filtering between fish of 70–79 mm and those of 80–89 mm, whereas the proportion in smaller fish was relatively constant. This finding indicated that gill-raker development may be complete by the time anchovy attain 80 mm SL, as suggested by King and Macleod (1976).

The size and the size range (5,0–20,0 mm) of prey consumed during active feeding were greater during this cruise than in April (0,5–2,0 mm). A similar predator-prey size relationship to that observed in the April data was evident, especially at midnight (Fig. 4d). In contrast to April, the widest range of prey sizes was consumed during the period of lowest trophic activity, when anchovies fed on other food types in the absence of euphausiids.

The predominance of large euphausiids, to the exclusion of other smaller potential prey in the stomach contents during active feeding (Figs 4c, d) demonstrates the importance of size-selective raptorial feeding in determining the diet of *E. capensis*.

WEST COAST, MAY 1983

Zooplankton provided the bulk of the contents during this cruise also, although phytoplankton's contribution was considerably greater than in either of the two cruises previously described, almost equalling zooplankton in importance in some instances (Fig. 5a). The data from fish with low fullness indices, reveal that phytoplankton made major contributions to the diets of smaller fish (Fig. 5a, 50–79 mm) and that the level of phytoplankton in the diet remained constant and apparently independent of fish length and hence degree of development of the gill rakers (Figs 5a, c). Phytoplankton made a similarly large contribution to the diets of larger fish with fuller stomachs (Figs 5a, c), but was sharply reduced in fish less than 80 mm SL.

Calanoid copepods were the major prey items during the low fullness phase except when (a) euphausiids (40–49 mm anchovy) and (b) phytoplankton (50–59 mm fish) were at their peak (Fig. 5c). During the high fullness phase, calanoid copepods were abundant in small fish but declined in importance with the coincident increase of phytoplankton and euphausiids in the stomachs of larger fish (Fig. 5c). The contribution by euphausiids to the diet during the low fullness phase was erratic and, although in one instance they provided 80 per cent of the total carbon, at no time was there more than one animal per stomach. Euphausiids supplied 30–50 per cent of the dietary carbon during the high fullness phase, increasing in importance with fish length (Fig. 5c). Again a few individuals per stomach made this large contribution.

Raptorial feeding behaviour was dominant in small fish, but filter-feeding increased in importance with increasing fish length (Figs 5b, d). The significant contribution by particles less than 0,5 mm to the diets of small fish in the low fullness phase (Fig. 5d) was a result of the presence of large cells of *Coscinodiscus* spp. (diameter 0,2–0,45 mm), the principal component of the phytoplankton contents, which were either actively consumed by raptorial feeding or passively retained, even by underdeveloped gill rakers. The decrease in copepod consumption with increasing fish length in the high fullness data (Figs 5c, d) was due to the longer fish preferentially preying upon the larger euphausiids while ignoring the smaller copepods. The phytoplankton present in the stomachs of the larger fish (> 70 mm) could be considered an incidental catch as the fish pursued the euphausiids, the steady increase in its importance with increasing fish length (Fig. 5c), reflecting the progression in gill-raker development.

SOUTH COAST, NOVEMBER 1983

Zooplankton dominated the stomach contents, phytoplankton making only an insignificant contribution (Fig. 6a). Calanoid copepods and euphausiids

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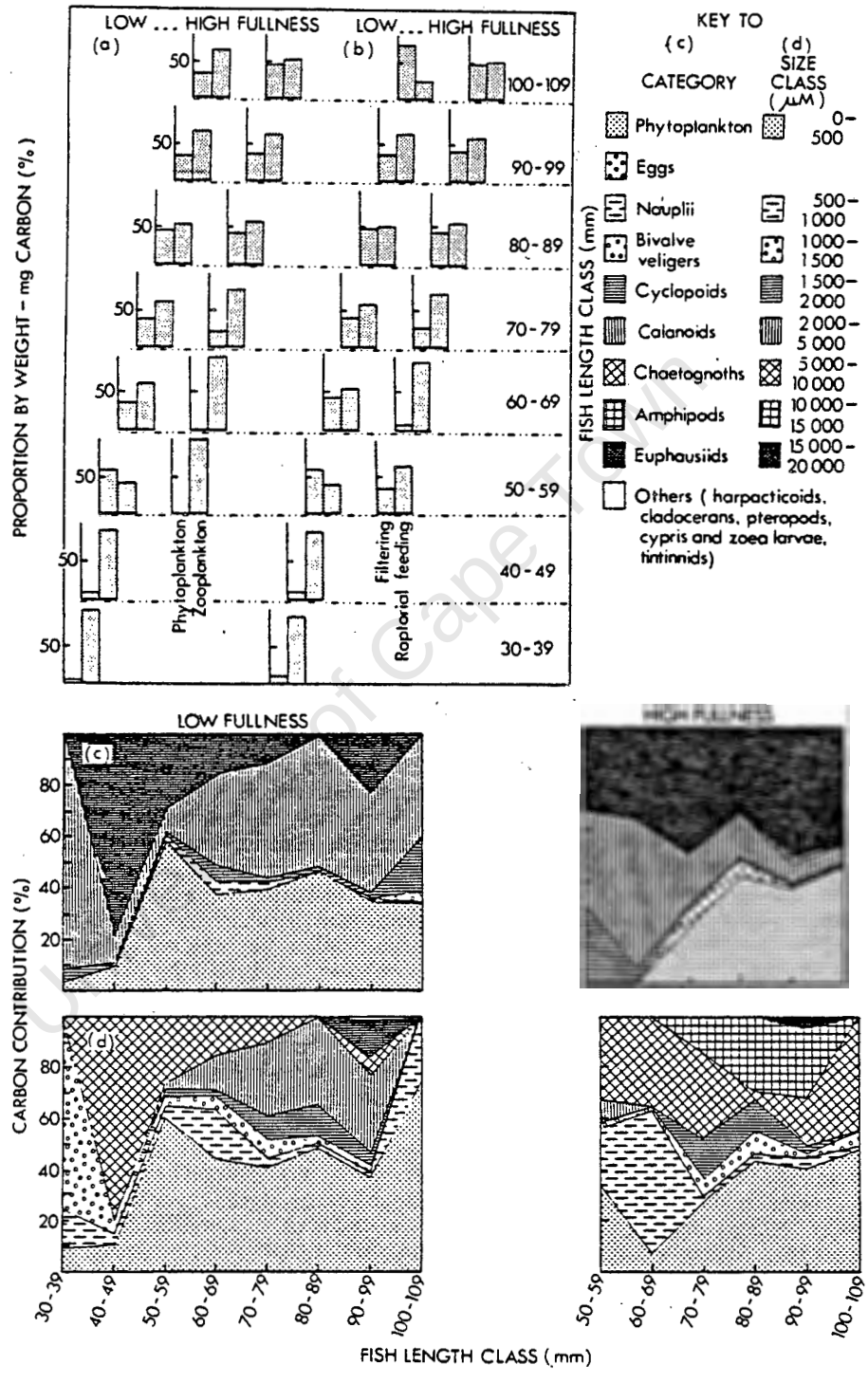

Fig. 5: (a) Proportions of zooplankton and phytoplankton in the stomachs; (b) proportions of stomach contents acquired by filter- and raptorial feeding; (c) prey composition in the diet; (d) prey size spectrum in the diet, all of *E. capensis* caught on the West Coast during May 1983

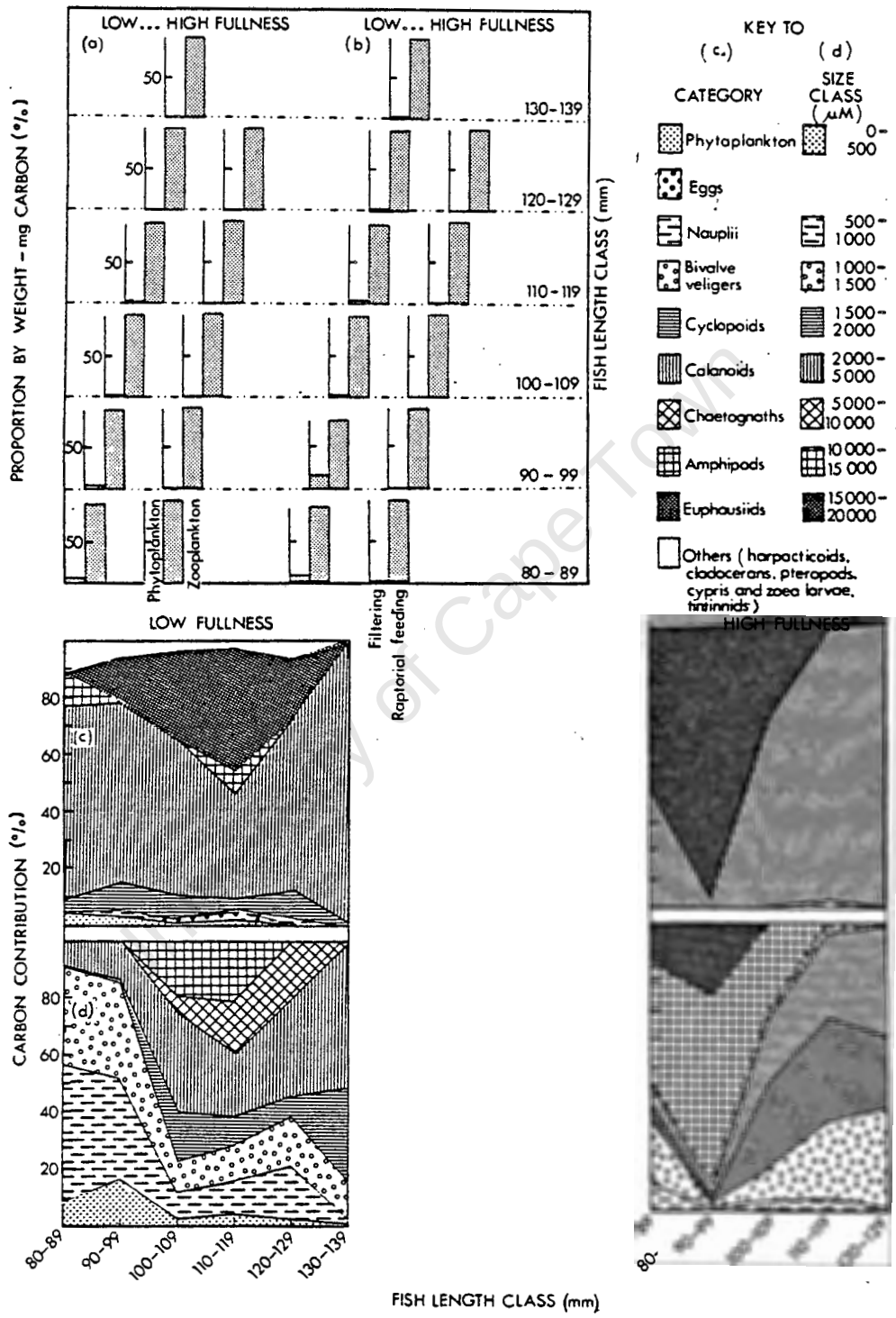

Fig. 6: (a) Proportions of zooplankton and phytoplankton in the stomachs; (b) proportions of stomach contents acquired by filter- and raptorial feeding; (c) prey composition in the diet; (d) prey size spectrum in the diet, all of *E. capensis* caught on the South Coast during November 1983

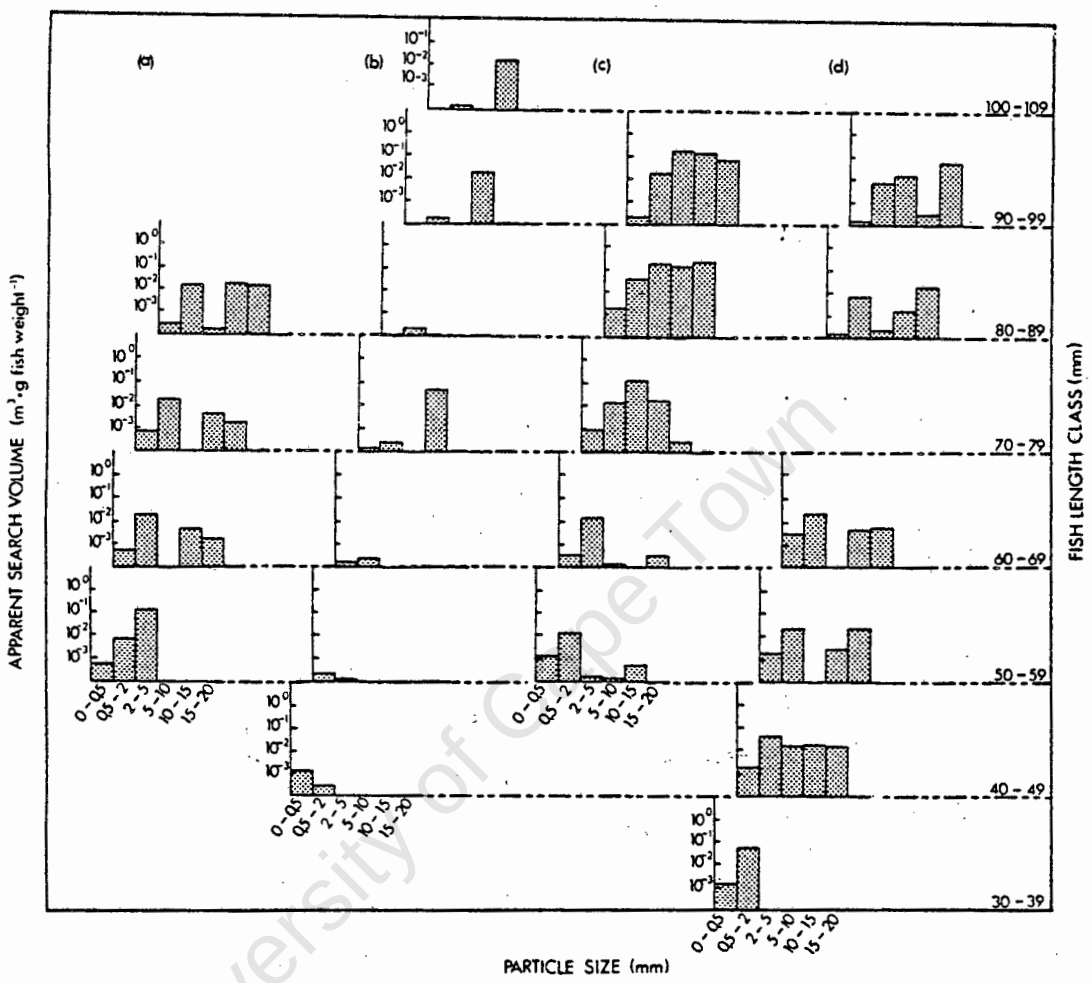

Fig. 7: Apparent search volumes for the prey size spectrum of *E. capensis* caught during (a) dawn, (b) midday, (c) dusk and (d) midnight sampling periods, April 1984

provided the bulk of the diet, the remainder originating from amphipods, cyclopoid copepods, crustacean eggs, nauplii and occasional fish eggs (Fig. 6c).

The bulk of the stomach contents was acquired by raptorial feeding (Fig. 6b), most of the prey being 1,0–10,0 mm maximum dimension (Fig. 6d). Despite the complete dominance of raptorial feeding behaviour, there is no clear predator-prey size trend such as was noted in the West Coast data (Fig. 6d).

Selectivity

Only data from April and May 1984 were used to investigate feeding selectivity. Poor spatial co-ordination between the trawl and plankton sample collections during the May and November 1983 cruises led to large disparities between the items in the stomachs and those in the plankton.

APRIL 1984

Similar trends to those noted in the prey particle-size data (Fig. 3d) were apparent in the ASV data (Fig. 7). Analysis of variance (ANOVA, Zar 1974) was employed to determine the significance of these trends (Table II).

During periods of low trophic activity, neither particle size fish length nor interaction of these two variables influenced the ASVs (Table II, Fig. 7). The

Table II: Results of the two-way ANOVA tests (Zar 1974) examining the influence of prey size (x) and predator length (y) on the apparent search volumes of the prey size categories in April 1984

Sampling period	Variable	F value	Significance
Dawn	x	0,67	Not significant
	y	0,46	Not significant
	$x*y$	0,024	Not significant
Midday	x	1,8	Not significant
	y	0,99	Not significant
	$x*y$	0,0045	Not significant
Dusk	x	2,38	Not significant
	y	4,92	Significant ($p < 0,05$)
	$x*y$	0,20	Not significant
Midnight	x	4,08	Significant ($p < 0,05$)
	y	0,57	Not significant
	$x*y$	0,014	Not significant

Table III: Results of the two-way ANOVA tests (Zar 1974) examining the influence of prey size (x) and predator length (y) on the apparent search volumes of the prey size categories in May 1984

Sampling period	Variable	F value	Significance
Dawn	x	2,90	Significant ($p < 0,05$)
	y	0,95	Not significant
	$x*y$	2,66	Significant ($p < 0,05$)
Midday	x	1,33	Not significant
	y	1,04	Not significant
	$x*y$	33,59	Significant ($p < 0,05$)
Dusk	x	10,28	Significant ($p < 0,05$)
	y	0,38	Not significant
	$x*y$	3,19	Significant ($p < 0,05$)
Midnight	x	2,93	Significant ($p < 0,05$)
	y	1,85	Not significant
	$x*y$	0,83	Not significant

insignificant effect of particle size on selectivity may be explained by non-selective filter-feeding being most prominent at these times. The present data do not indicate a relationship between feeding selectivity and fish length, such as described by King and Macleod (1976, Table II).

During periods of higher trophic activity, when raptorial feeding prevails, fish length (dusk) and particle size (midnight), though not the interaction of the two, significantly influenced the selectivity values (Table II). The significant value for fish length at dusk was due to the occurrence of euphausiids and amphipods in the stomachs of the larger fish (Fig. 3c). This result only occurred once (Tables II and III) and is therefore difficult to interpret. Whereas the ASV data for dusk (Fig. 7) suggest that selection increases with particle size and that longer fish tend to select for larger particles during active raptorial feeding, no statistically significant relationships were found (Table II). The effect of particle size on the selection values at midnight is evident in Figure 7. This result is similar to the findings of laboratory and field studies on size-selective raptorial feeding of engraulids (Leong and O'Connell 1969, O'Connell 1972, Koslow 1981, Angelescu 1982) and mesopelagic zooplanktivores, all of which are visual predators (Clarke 1980, 1982, Baird and Hopkins 1981, Hopkins and Baird 1985).

MAY 1984

Compared with April, the trends observed in the prey particle size data (Fig. 4d) are more apparent in the ASV data for May (Fig. 8).

During the period of reduced feeding activity, neither particle size nor fish length affected selectivity (Table III), although there was a significant interaction between the two variables. This result is consistent with that of April, indicating that there is no apparent selective feeding behaviour when filter-feeding is prevalent.

During periods of enhanced raptorial feeding activity, particle size, but not fish length, influenced selectivity (Fig. 8, Table III). These results are similar to those obtained for the midnight sample period in April (Fig. 7, Table II). The significant values for the prey- and predator-dimension interactions indicate that prey selection is a function of both prey size and fish length, with the longer fish apparently selecting for larger particles (Fig. 8, Table III). This functional relationship was not observed in the April data set, probably because of the more limited size range of prey available during that cruise.

DISCUSSION

Feeding periodicity

The feeding cycle determined for *E. capensis* from the West Coast cruises is similar to those described for *E. anchoita* (Angelescu 1982) and *E. mordax* (Longhurst 1971). King and Macleod (1976) give no indication of a diel feeding cycle in their preliminary study. Diel feeding patterns are common among mesopelagic zooplanktivores (Clarke 1978, 1980, Hopkins and Baird 1981, 1985). The present results and those of Angelescu (1982) differ from many in the literature. Baxter (1967) stated that anchovies are generally recognized as daytime feeders. Loukashkin (1970) observed that stomachs of *Engraulis mordax*

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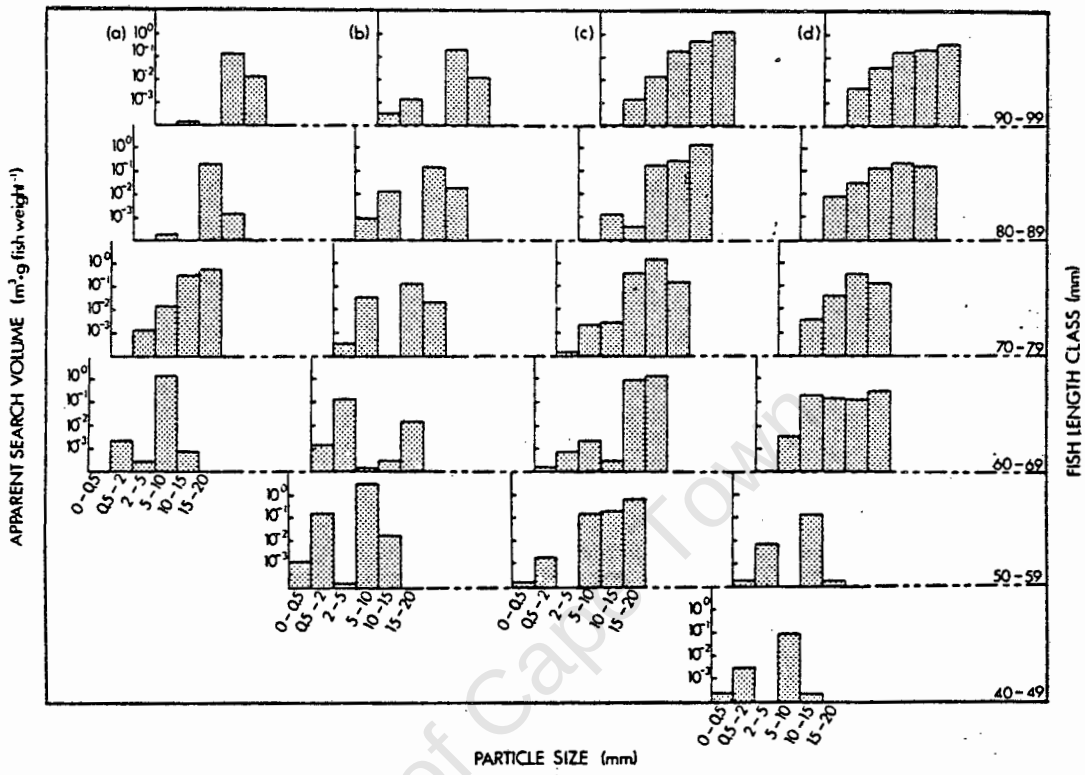

Fig. 8: Apparent search volumes for the prey size spectrum of *E. capensis* caught during (a) dawn, (b) midday, (c) dusk and (d) midnight sampling periods, May 1984

were fullest during the day, and Koslow (1981) studied the feeding selectivity of *E. mordax* by observing actively foraging shoals during the day.

On South Africa's west coast, the diel feeding cycle was associated with a marked vertical migration and changes in shoaling behaviour (Fig. 9). During the day, anchovies formed dense shoals in the midwater and demersal layers. At dusk these shoals rose and dispersed, forming a diffuse layer in the surface waters shortly after dark, which coincided with the peak in stomach fullness and the predominance of raptorial feeding. The fish remained scattered until dawn, when trophic activity declined and filtering increased in importance as they began migrating to deeper water and re-aggregating into the dense shoals characteristic of daytime behaviour. This cycle was not noted by King and Macleod (1976). Angelescu (1982) observed that intensive "mixed feeding" accompanied the diffusion of shoals of *E. anchoita* and their ascent to the upper water column, whereas the descending, aggregating movements were associated with reduced feeding activity dominated by the filtering mode. Longhurst (1971) stated that there was acoustic evidence that *E. mordax* executed nocturnal vertical migrations and Loukashkin and Grant (1965) observed that *E. mordax* always preferred lower light intensity during experiments with contrasting intensities of white light, suggesting a trigger mechanism for nocturnal vertical movements. O'Connell (1963) found that the retinae of the eyes of *E. mordax* were well adapted to visual predation at low light levels such as might be encountered at night in surface waters. The migration and feeding patterns of these fish are associated with the diel vertical movements of their mesozooplanktonic prey, e.g. the larger calanoid copepods and euphausiids, which also ascend from the bottom to the surface layers in the evening and are hence most accessible to predators at this time (Hutchings 1985, Pillar in prep., Verheye and Hutchings in prep.).

Feeding chronicity will not always be as regular as was noted on the three West Coast cruises. Anchovies are opportunistic foragers (Schoener 1971, Angelescu and Anganuzzi 1981, Angelescu 1982) and will feed

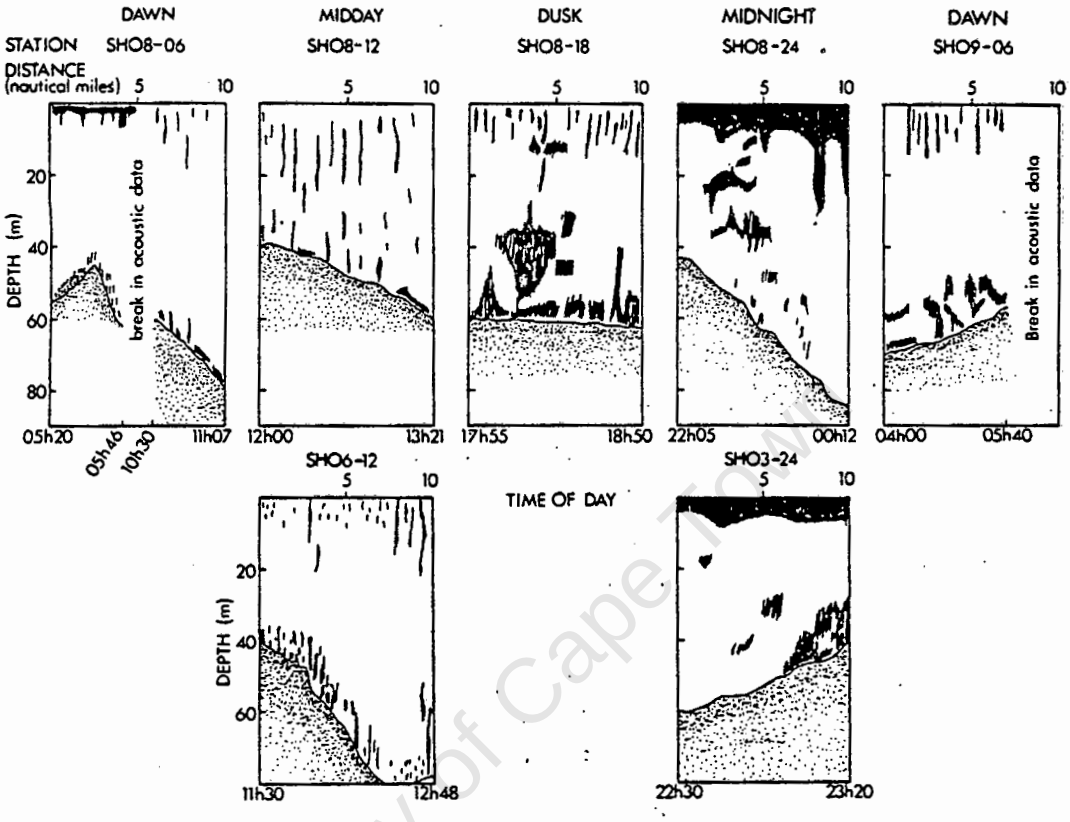

Fig. 9: Sketches of acoustic traces of anchovy shoals made with a 38-kHz echosounder on 16 and 17 April 1984, illustrating the ascent and dispersion of shoals after dark coinciding with increased feeding activity, followed by aggregation and descent associated with low feeding activity during daylight. Two additional sketches from the earlier stations are also shown

whenever suitable prey are encountered, e.g. Station 124–04A in November 1983. Opportunistic feeding has obvious advantages in assisting the fish to fulfil their nutritional requirements in such a heterogeneous environment as the southern Benguela.

The 6-h phase-shift in the feeding cycle observed in the South Coast data agrees with the findings of Shelton and Hutchings (1982) and Hampton *et al.* (1985) on the diel spawning and migration patterns of *E. capensis*. Similar spawning patterns have been noted for *Sardinops caerulea* (Ahlstrom 1959) and *E. mordax* (Hunter and Macewicz 1980). The spatial and temporal separation of spawning and foraging must act to reduce the impact of egg cannibalism. The cycle noted during the present study differs from that of Valdés *et al.* (1987), who found peak fullness to be at sunset (19h00) and the lowest values at sunrise (04h00–05h00). Those samples were collected in a restricted geographical area on the offshore reaches of the Agulhas Bank, primarily for the investigation of egg cannibalism. The unusually high egg densities encountered were considerably above those required to initiate filter-feeding in *E. mordax* (Hunter and Dorr 1982) and this fact, in conjunction with the low zooplankton biomass observed, could account for the differences in feeding behaviour. The data of Valdés *et al.* (op. cit.) may therefore be considered a special case and not germaine to broader generalizations on feeding periodicity. It is interesting to note that feeding activity, as deduced from stomach fullness, was low during the peak spawning period in both the present study and that of Valdés *et al.* (op. cit.). The protracted feeding period and the more frequent opportunistic feeding observed on the South Coast may be an effort by the fish to offset the high energy costs of serial spawning. Hunter and Leong (1981) calculated that an average daily ration of copepods equivalent to 4–5 per cent of

chosen measure is that, having units, the results give an indication of the effort expended to obtain food items. Thus, these data may be combined with laboratory work on feeding rates, selectivity and energetics to construct energy budget models of some ecological significance for *E. capensis*.

The sources of error inherent in field-based selectivity studies are due primarily to the sampling procedures. The scale of sampling is critical. Anchovy are microscale samplers of the plankton, able to take advantage of small aggregations of prey. It is therefore necessary to sample the potentially available food on a similar scale. This is impossible, because most plankton-sampling methods integrate plankton densities over tens of cubic metres. This mismatch of sampling scales leads to large errors in the calculated selection values, especially when the major prey types are known to aggregate (Alldredge *et al.* 1984, Nicol *et al.* 1987). The sampling of fish with a large trawl also presents problems, because the location of fish within the shoal cannot be determined. This information will be important if the fish at the leading edge of the shoal remove significant quantities of the larger prey items, leaving only the smaller items for the following fish to capture. Their flexible feeding behaviour allows anchovies to select for the smaller items in the absence of larger prey (Koslow 1981). This factor will tend to blur any selection index. Avoidance of the sampling gear by larger prey (Brinton 1967) and poor spatial co-ordination between fish and plankton sample collections are also key sources of error.

Many factors, both biological and physical, affect the selective feeding behaviour of fishes, the most important of which are prey size and predator length (Leong and O'Connell 1969, O'Connell 1972, O'Brien *et al.* 1976, Clarke 1980, Baird and Hopkins 1981, Koslow 1981, Angelescu 1982, Hopkins and Baird 1985, Main 1985). The present data agree with these results. The data also suggest that taxonomy may play a secondary role in selection, mainly through the size differences of different prey types. Any other effect of taxonomy is masked by the methods of prey identification used. Clarke (op. cit.), Baird and Hopkins (op. cit.) and Hopkins and Baird (op. cit.) noted that taxonomy had a secondary effect on prey selection, and Koslow (op. cit.) observed enhanced selection of *Calanus pacificus* by *E. mordax* on one occasion, though he did not interpret the significance of this result.

Bearing in mind the above-mentioned sources of error, several conclusions can be drawn from the data. Selective raptorial feeding is dominant and selection increases with prey size and predator length. This relationship suggests there may be an increase in the trophic niche breadth with increasing predator length. Examples of this relationship are common in the literature (Brooks and Dodson 1965, Rojas de Mendiola 1974, Popova 1978, Villiers 1980, Hunter 1981, McCullough and Stanley 1981, Cohen and Lough 1983, Govoni *et al.* 1983). The size-selective raptorial feeding on zooplankton and the influence of predator length observed in this study have been recorded in the laboratory (Leong and O'Connell 1969, O'Connell 1972, Gibson and Ezzi 1985) and in the field (Nakai *et al.* 1962, Cushing 1978, Angelescu 1982) for other planktivores. Koslow (1981) stated that *E. mordax* fed size-selectively on zooplankton, but he found no significant difference in the selectivity of two schools composed primarily of 0-group and II-group fish respectively. Many authors considered anchovies to be non-selective omnivores, only displaying selective behaviour as larvae and juveniles (Yamashita 1957a, b, Walsh 1981, and others reviewed in Cushing 1978 and James 1984). The diet composition and selectivity data of April and May 1984 clearly illustrate that the anchovy are opportunistic foragers, selecting for the largest prey available over a considerable size range. Koslow (op. cit.) obtained a similar result for *E. mordax*.

This finding is of some ecological significance, because it allows the prediction of the anchovies' diet from data on particle-size spectra collected during plankton sampling cruises (Verheye in prep., Verheye and Hutchings in prep.). These predictions are useful for modelling energy budgets and, even more important, for elaborating the major pathways for the transfer of energy through the food chain to commercial fish stocks and higher predators.

SUMMARY

1. *Engraulis capensis* displays a marked synchronicity in feeding activity associated with changes in vertical distribution in the water column and in shoaling behaviour.
2. The major component of the diet is mesozooplankton, especially calanoid copepods and euphausiids of 1,0–20,0 mm, with a higher incidence of predation on 1,0–15,0 mm organisms.
3. Raptorial feeding is the predominant mode of feeding.
4. *E. capensis* displays extremely flexible feeding behaviour and a high degree of opportunism in fulfilling its dietary requirements, alternating its modes of search and intake depending upon the level of trophic activity and the spectrum of

available food.

5. There is no change in feeding behaviour with increasing fish length.
6. *E. capensis* selects its food primarily on the basis of prey size, this selective capacity being dependent upon predator length.
7. *E. capensis* is a secondary consumer in the southern Benguela, direct grazing upon the primary producers being of only minor importance.

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CHAPTER THREE

The capture and transfer of wild *Engraulis capensis* to the laboratory and notes upon the maintenance of laboratory populations of wild pelagic fish.

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METHODS OF CAPTURE AND TRANSFER TO THE LABORATORY OF WILD PELAGIC FISH

A. G. JAMES, L. HUTCHINGS*, C. L. BROWNELL† AND D. A. HORSTMAN**

Two successful methods of capturing anchovy, pilchard and other pelagic fish and transporting them to the laboratory are described.

Twee suksesvolle metodes vir die vang van ansjovis, sardyn en ander pelagiese vis en hulle vervoer na die laboratorium word beskryf.

In recent years much laboratory research has been focused on the Cape anchovy *Engraulis capensis* and the South African pilchard *Sardinops ocellatus*. However, this work has been hindered by a shortage of suitable experimental fish. Initially material was provided by laboratory rearings from wild eggs, but the cost and the effort involved in producing large numbers of juveniles and adults by this method are restrictive.

Attempts to capture wild juvenile and adult fish and to transport them to the laboratory had been made by personnel from the Sea Fisheries Research Institute, but they had met with little success. The method of capture used, purse-seining, severely stressed and damaged the fish and none were brought to the laboratory alive. Local bait-boats have also tried to store pelagic fish alive for tuna fishing, but they have been unsuccessful in retaining them for more than a few days. The scales of both anchovy and pilchard are shed easily when contact is made with solid objects such as nets, tank walls and other fish. This makes them vulnerable to bacterial infections.

Although there are several published methods for capturing, transferring and maintaining pelagic fish in the laboratory, most descriptions are concerned primarily with either the special equipment (Hettler 1983) and conditions required for long distance transport (McFarland and Norris 1958, McFarland 1960), with the maintenance of established laboratory populations (Tardent 1962, Hope 1982) or with the capture of large fish (Arté 1966). Few provide even a brief description of a simple but successful method of capturing and transferring small clupeoids (Verheijen 1956).

This note describes in detail two successful procedures for the capture of anchovy, pilchard and other pelagic fish and their transportation from the fishing harbour to the laboratory (Fig. 1).

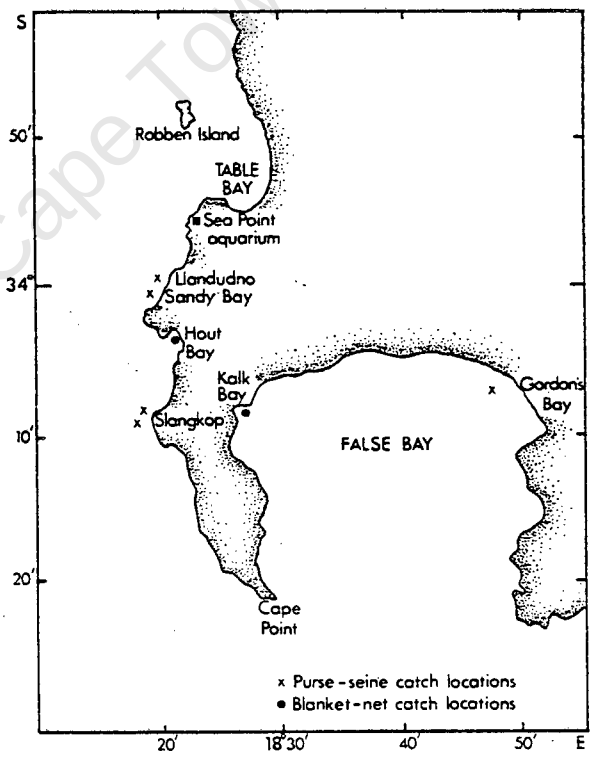

Fig. 1: The Cape Peninsula, showing the catch position and the location of the research laboratory aquarium and some places mentioned in text

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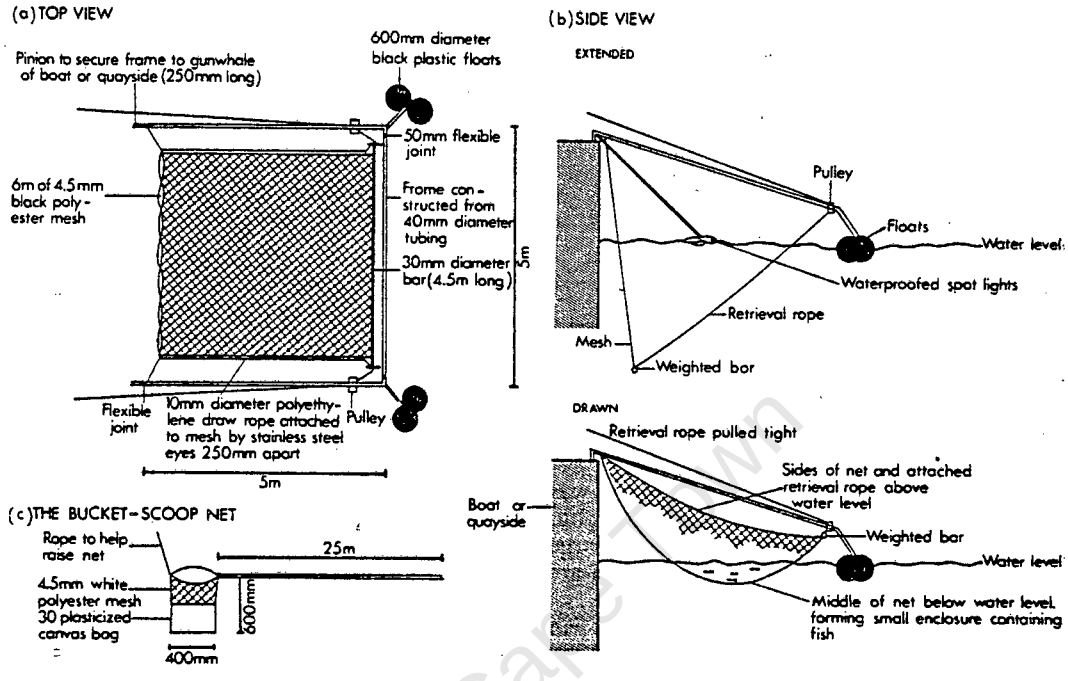

Fig. 2: The blanket net

METHODS AND MATERIALS

The two methods devised to catch pelagic fish were aimed at different life stages, juveniles and adults. The former were caught with a blanket net and the latter by means of a modified version of the original purse-seine method.

The blanket net

This net (Fig. 2) constructed for use off either a 7-m skiboat or harbour walls and quays using a design modified from that of Radovich and Gibbs (1954). The net is hung vertically in the water and three spotlights (modified automobile fog-lamps in waterproof casings operated by a 12-V car battery) allowed to float on the water surface. The lights attract zooplankton, which rapidly form a dense patch immediately beneath them. Usually within 1,5 h, small shoals of juvenile anchovy, pilchard, horse mackerel *Trachurus capensis* and other fish arrive and start feeding on the zooplankton. When there are sufficient fish gathered in the illuminated area, the net is rapidly drawn to the surface, trapping the fish in a shallow enclosure (Fig. 2b).

The trapped fish are transferred by means of a bucket-scoop net (Fig. 2c) into 100-*l* covered plastic bins (Fig. 3) filled with seawater being lightly aerated by two portable 12-V compressors operated off a car battery. Heavy aeration stressed the fish and increased mortality. Because of the short time required to fill the bins with fish and take them to the laboratory, it was not considered necessary to ensure a constant flow of seawater to the bins. Each 100-*l* bin can hold up to 70 juvenile fish.

At the laboratory, the fish are transferred to aerated, open-system flow-through plastic tanks of diameter 2 or 3 m. They are initially best kept in subdued light at a temperature of about 17,5°C.

On the three occasions (Table I) when this method of capture and transfer was employed, about 50 per cent of the captured fish survived the first night of captivity. It was evident that mortality was especially high among specimens smaller than 35-mm standard length L_c. Additional mortalities were experienced in the first 5–7 days following capture (Table II), but thereafter mortality was low. Some 240 anchovy, 100 pilchard and 70 horse mackerel were kept successfully in the laboratory for eight months after collection by this method.

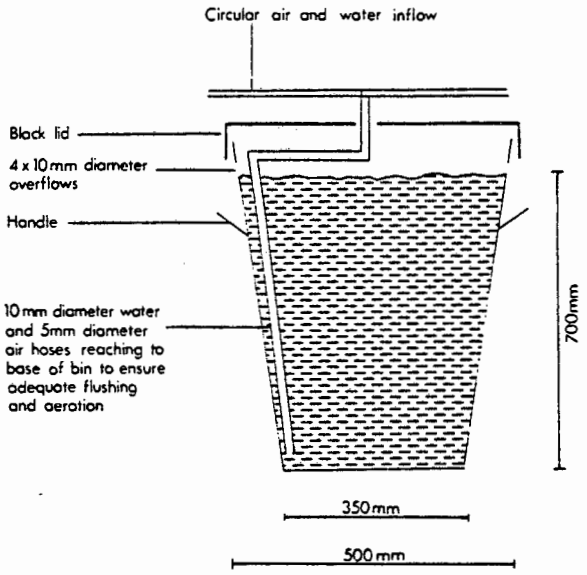

Fig. 3: The 100-*l* transfer bins

Table II: Levels of survival and daily rates of mortality of anchovy (56 mm mean L_c) taken to the laboratory on 1 April 1985 during their first fourteen days in captivity

Day after capture	Survival (%)	Percentage mortality per day
0	100,0	-
1	92,0	8,0
2	83,6	16,4
3	81,2	2,9
4	80,0	1,5
5	80,0	-
6	79,6	0,5
7	78,8	1,0
8	78,8	-
9	78,8	-
10	78,4	0,5
11	78,4	-
12	78,0	0,5
13	76,0	1,0
14	76,0	-

The purse-seine method

This method is used to obtain adult fish and necessitates the use of a purse-seine vessel equipped with a 12,5-mm mesh anchovy net.

When a small shoal of anchovy or pilchard is located by sight or echo-sounder the net is set around it and pursed. When pursing is complete and approximately 75 per cent of the net has been drawn aboard, the seining operation ceases. At this point the net forms a small shallow enclosure with the shoal concentrated within. The boat and net are then manoeuvred to make the fish accessible to brailling with the bucket-scoop net. This stage is critical because if the net is drawn too tight the fish collide with the net and lose their scales. The object is to keep the fish moving freely in the net in a small tight shoal, yet concentrated enough to make them easy to catch. With the bucket-scoop net the fish are transferred a few at a time into the 100-*l* bins. By trial and error it was found that 2–10 fish could be moved in each scoop. A net without a solid bag caused excessive scale-losses and subsequent high mortality. The critical factor is preventing the fish from touching any solid object, be it the net or each other.

Each 100-*l* bin can hold 40–50 adult anchovies or 15–20 adult pilchards for up to 8 h. They are covered as soon as the fish have been introduced. Initially they were aerated by means of the 12-V compressor, but this resulted in the formation of a dense layer of foam (caused by mucus secretions from the agitated fish) and scales on the surface of the water which clogged the gills of the fish. In addition, the compressor and battery proved to be unreliable and cumbersome at sea and aeration was replaced by a clean seawater flow-through supplied from the boat's deck-wash at a rate of 5–6 $l \cdot min^{-1}$. This high rate of flow ensured that the water in the bins remained at approximately constant temperature and that there was an adequate supply of oxygen for the fish during the return trip.

While steaming back to harbour, the bins are frequently inspected to ensure that a constant high rate of flow of seawater is maintained and to remove any dead or moribund fish. Damaged fish and fish suffering from heavy scale-loss are easily identified by the patches of darkened skin on their flanks and by their abnormal swimming behaviour (Verheijen

Table I: Blanket-net collections of live fish

Date	Location	Species collected
9/11/84	Kalk Bay harbour	*Sardinops ocellatus* *Trachurus capensis* *Etrumeus whiteheadi* *Mugil cephalus* (Mullet)
13/11/84	Kalk Bay harbour	*Pomatomus saltatrix* (Elf)
1/4/85	Hout Bay harbour	*Engraulis capensis* *Sardinops ocellatus*

Table III: Purse-seine catches of live fish

Date	Location*	Vessel	Mesh size (mm)	Species caught	Time spent in bins (h)	Number of fish returned
16/6/85	Llandudno	*Rijger*	12,5	Anchovy Pilchard	3	511 43
20/6/85	Sandy Bay	*Rijger*	12,5	Anchovy Pilchard	3	106 24
1/7/85	Slangkop	*Rijger*	12,5	Anchony Pilchard	3	204 31
9/1/86	Slangkop	*Trudy Marleen*	32,0	Pilchard	7	93
24/1/86	False Bay	*Sherene*	12,5	Anchovy Pilchard Elf	4,5	142 28 9

* See Fig. 1

1956).

At the quayside, the seawater flow is terminated and 1,6 mg·l^{-1} veterinarian tetracycline (active ingredient 5,5-per-cent tetracycline hydrochloride manufactured by Glaxo [Pty] Ltd) is added to the water. This procedure was only adopted after the drug's effectiveness had been demonstrated by treatment of the first two batches of fish taken to the laboratory (James *et al.* 1988). The bins are lightly aerated while being transported to the laboratory.

In the laboratory the fish are transferred into plastic tanks. Up to 250 fish may be accommodated in a 2-m diameter tank (volume 3 141*l*) and 400 in a 3-m tank (volume 4 948*l*). The tanks are connected to an open flow-through system with an initial flow rate of approximately 1 *l*·min^{-1}, which is increased to 4–5 *l*·min^{-1} after the termination of tetracycline treatment. Each tank is dosed with 1,6 mg·l^{-1} tetracycline and the initial dose is supplemented three times daily to maintain this concentration in the tank during the first 4–6 days of occupation (James *et al.* 1988). Again, this procedure was only adopted on the third trip. If a bacterial infection breaks out and cannot be controlled, all fish are removed and the tank sterilized with industrial bleach. During this initial period in captivity, when mortality is at its peak, any fish displaying symptoms of infection, such as bulging eyes, blindness or discoloured skin

Table IV: Survival levels and rates of mortality during the first fourteen days in captivity for the first three batches of anchovy returned to the laboratory

Days after capture	Survival (%)	Percentage mortality per day	Survival (%)	Percentage mortality per day	Survival (%)	Percentage mortality per day
	16.6.85		20.6.85		1.7.85	
0	100	0	100	0	* 100	0
1	84,9	15,1	96,2	3,8	97,5	2,5
2	63,8	24,9	89,6	6,9	95,6	2,0
3	* 40,7	36,2	83,0	7,4	88,7	7,2
4	30,3	25,5	71,7	13,6	86,8	2,2
5	25,4	16,1	* 66,3	17,1	85,3	1,7
6	24,5	3,8	56,6	4,8	* 84,3	1,1
7	24,3	0,8	56,6	-	84,3	-
8	* 24,3	-	56,6	-	84,3	-
9	24,3	-	56,6	-	84,3	-
10	24,3	-	* 56,6	-	84,3	-
11	24,3	-	56,6	-	84,3	-
12	24,1	0,8	56,6	-	84,3	-
13	24,1	-	56,6	-	84,3	-
14	24,1	-	56,6	-	84,3	-

* Initiation and termination of antibiotic treatment

(James *et al.* op. cit.), are immediately removed from the tank.

The fish are fed twice daily on a mixture of live food (copepods and *Artemia salina*) and an artificial food based on vitamin-enriched frozen anchovy or pilchard. The fish are maintained either under natural light or an artificial 12-h light, 12-h dark cycle, and they are ready for use in experiments within 21 days.

RESULTS AND DISCUSSION

Both methods described proved useful in providing fish to restock laboratory populations, though more effort was directed towards improving the purse-seine method and increasing the survival of the captured adult fish. Fish were obtained by purse-seine on five separate occasions (Table III) and survival improved from approximately 25 per cent to more than 80 per cent (Table IV). One of the major problems encountered with the use of bait-boats was their multi-purpose role: the vessels fish not only for anchovy but also for line- and gamefish and rock lobster, making them unavailable for collection of live fish for a large portion of the year. However, because of the success in maintaining these fish in the laboratory, the collection trips can be planned well in advance.

These simple procedures have proved more than adequate in fulfilling the requirements of current research and no supply problems are foreseen in the future.

ACKNOWLEDGEMENTS

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1988

A NOTE ON THE INCIDENCE AND TREATMENT OF A BACTERIAL INFECTION OF WILD PELAGIC FISH MAINTAINED IN THE LABORATORY

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The pathogens of an eye infection affecting capture-stressed pelagic fish were isolated and identified. Prophylactic use of veterinarian tetracycline was found to be an effective treatment.

Die patogene van 'n oog-ontsteking by pelagiese vis wat aan vangspanning blootgestel is, is afgesonder en geëien. Voorkomende gebruik van veeartsenykundige tetrasikline het 'n doeltreffende behandeling geblyk.

Wild anchovy and pilchard captured and transported to the laboratory contracted a bacterial infection causing varying levels of mortality. This paper describes the symptoms of the disease and the isolation and identification of the pathogens and treatment of the disorder.

SYMPTOMS

Approximately 24 h after capture, affected fish begin to lose their natural colouration and exhibit abnormal swimming behaviour. Within 48 h, widespread haemorrhaging is evident on the snout and flanks. The eyes of infected fish swell and, in severe cases, become dislocated from the eye sockets. The fish are virtually moribund, hanging motionless just below the water's surface or swimming slowly in tight circles. The eyes may burst 30–36 h after beginning to distend, releasing a watery blood-coloured fluid.

In most instances this disease is fatal, most of the victims dying shortly before or after the disintegration of the eyes. The blind survivors have impaired swimming capabilities, making them unsuitable for experimental work.

ISOLATION AND IDENTIFICATION OF PATHOGENS

Specimens of eye fluid from infected fish were collected on sterile cottonwool swabs, streaked onto Blood Agar (Cowan and Steel 1965) and incubated at 23°C for 48 h. Three isolates were identified on the basis of colony morphology and streaked to purity on Blood Agar. Pure colonies were then inoculated onto MacConkey's Agar, EMB-Levine Agar. DNAse Agar, BTB-Teepol Agar, PXA Agar, BHI Agar and Gelatin Agar and incubated at 23°C for 48 h. Colonies grown on Gelatin Agar were tested with Frazier's solution to assess gelatin liquefaction. The three isolates were tested in Glucose Hugh-Leifson Oxidative/Fermentative medium and in an alkaline (pH 8,0) nutrient broth. All isolates were further tested with API 20E identification tests (*Appareils et Procedes d'Identification, Montalieu Vercieu*) following the methods recommended by the manufacturer. The results of all identification tests are presented in Table I.

Isolate 1

This isolate was a non-motile, Gram-negative coccoid rod which produced haemolytic colonies on Blood Agar and liquefied gelatin. Identification proved difficult. The majority of the tests suggested that it was *Acinetobacter calcoaceticus* var. *anitrificans*. However, the isolate displayed positive oxidase activity, indicating that it may be a *Pseudomonas* species although it was non-motile. Bøvre and Hagen (1981) stated that *A. calcoaceticus* is commonly found on mucosal surfaces of fish and suggested that it may occasionally be responsible for infections, though its pathogenicity is low. Pseudomonads, which are common in marine environments, may also act as pathogens and have been implicated in

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Table I: The results of the identification tests used to differentiate between the three isolates

Test	Results		
	Isolate 1	Isolate 2	Isolate 3
Blood Agar — haemolysis	+	−	+
MacConkey Agar — growth	−	+	+
EMB-Levine Agar — growth	−	+	−
DNAse Agar — growth	+	−	−
BHI Agar — growth	−	−	−
BTB — teepol — growth	+	*	+
PXA Agar — growth	+	−	+
Glucose — oxidative	+	+	+
Glucose — fermentative	−	+	+
pH 8,0 — growth	+	*	+
ONPG	−	+	+
ADH	−	−	+
LDC	−	−	−
ODC	−	−	−
CIT	−	−	−
H_2S	−	−	−
Urease	−	−	−
TDA	−	−	−
Indole	−	+	+
Voges — Proskauer	−	−	+
Gelatinase	+	−	+
Mannitol O/F	−	O/F	O/F
Inositol O/F	−	−	−
Sorbitol O/F	−	−	−
Rhamnose O/F	−	−	−
Sucrose O/F	−	−	−
Melibiose O/F	O	O/F	O/F
Amygdalin O/F	O	O/F	O/F
Arabinos O/F	O	O/F	O/F
Oxidase	+	−	+
Catakase	+	+	+
Nitrate reductase	+	+	+
Motility	−	−	+
Gram	−	−	−
Form	Coccoid rod	Coccoid rod	Rod

\+ positive
− negative
* result ambiguous
O oxidative only
O/F oxidative and fermentative

secondary infections where resistance is reduced (Bergan 1981).

Isolate 2

This was a non-motile, Gram-negative coccoid rod which displayed negative reactions to the Blood Agar and Gelatin liquefaction tests. It was positively identified as *Enterobacter agglomerans*, but this group is poorly differentiated (Brenner 1981) and few sources provide an adequate characterization. Brenner (op. cit.) states that *E. agglomerans* is documented as an opportunistic pathogen responsible for secondary infections in wounds and for septicaemia in cases of low resistance.

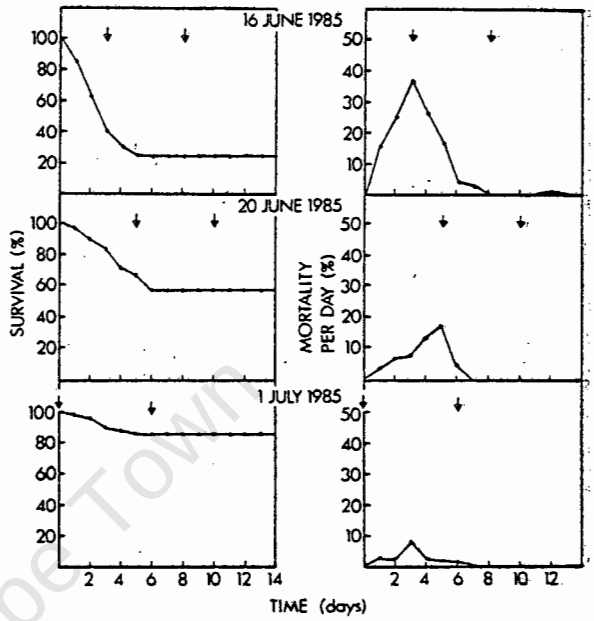

Fig. 1: Levels of survival and daily rates of mortality for the first three batches of fish transported to the laboratory (arrows indicate initiation and termination of antibiotic treatment)

Isolate 3

This isolate was a motile, Gram-negative rod displaying haemolytic activity on Blood Agar and capable of gelatin liquefaction. A positive API identification as *Aeromonas hydrophila* was made, with the caveat that this strain did not appear to produce gas from glucose fermentation. This suggests that, whereas the generic classification is valid, the specific identification may be incorrect. Specific identifications of the *Aeromonas* group are in a state of flux (Sakazaki and Balows 1981). The absence of gas production and a positive Voges-Proskauer reaction suggest that the isolate may be *Aeromonas caviae*.

This last-named genus is a common component of aquatic systems and may exist as an intestinal or kidney symbiont in fish. It is widely implicated in outbreaks of disease in fish and amphibians, producing bacteremia and the severe haemorrhagic syndrome known as Red Sore Disease in stressed populations (Bullock 1961, Shimizu 1969, Shotts *et*

Table II: Sensitivity of the three isolates to four antibiotics

Antibiotic*	Diameter of zone of sensitivity (mm)		
	Isolate 1	Isolate 2	Isolate 3
Streptomycin (25 μg)	26	38	-
S3 300 (25 μg)	-	-	35
SXT (25 μg)	-	21	30
Tetracycline (5 μg)	16	26	36

* The values in parentheses indicate the doses used for the sensitivity tests

al. 1972, Sakazaki and Balows 1981). Because of the similarities between the observed symptoms and those described for Red Sore Disease, this isolate was considered to be the main causative agent of the infection.

TREATMENT

The sensitivity of the three isolates to four readily available antibiotics was tested. Veterinarian tetracycline (active ingredient 5,5-per-cent tetracycline hydrochloride by weight, manufactured by Glaxo [Pty] Ltd) produced the most satisfactory results (Table II).

The tetracycline was added to the water of the fish tanks at concentrations of 1,6 mg·l^{-1}. The tanks were dosed three-times daily at 8-h intervals to maintain this concentration because the tanks had a constant flow-through of clean seawater. Suspending the antibiotic in the water was found to be the most effective method of ensuring that all the fish were exposed to its action. Attempts to coerce the fish to consume the drug by mixing it with their food proved to be unsuccessful as most of the fish do not eat for several days after being transferred to the laboratory (James *et al.* 1988).

The antibiotic was administered to the first two batches of fish (16 and 20 June 1985) only after they had been in the laboratory for 3 and 5 days respectively and had already suffered high mortality (Fig. 1). The third (1 July 1985) and subsequent batches were dosed immediately after capture. Treatment was continued until mortality had been reduced to below 1,0 per cent per day (Fig. 1). The results shown in Figure 1 clearly illustrate that tetracycline is effective in preventing capture-stressed fish from suffering heavy mortality due to *Aeromonas* spp. and other bacterial pathogens. In all cases, mortality was reduced to low levels after treatment with the antibiotic. In the third batch, most of the mortality can be accounted for by the removal of damaged fish from the tank.

The treatment of this infection is, by necessity, a cure rather than a preventative measure. Treatment must begin immediately after capture, and badly damaged fish, which are most likely to succumb to the infection, should be removed from the tanks.

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CHAPTER FOUR

The effect of particle size and concentration on the feeding behaviour, selectivity and rates of ingestion of food by the Cape anchovy *Engraulis capensis* Gilchrist.

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INTRODUCTION

Engraulis capensis forms the mainstay of the South African and Namibian purse seine fisheries. Early field work had indicated that the larvae and juveniles were selective, raptorial carnivores but switched to non - selective filter feeding omnivory when adults (Robinson 1966; King and Macleod 1976). Later work refuted these findings, showing that the anchovy, although a facultative filter feeder, practiced size - selective carnivory throughout its life history (Chapter two).

Previous laboratory work on planktivorous fish had indicated that feeding behaviour and the rate of consumption of food were dependent upon the size and density of the available prey (Leong and O'Connell 1969; O'Connell 1972; O'Connell and Zweifel 1972; Durbin and Durbin 1975; Janssen 1976; Holanov and Tash 1978; Hunter and Dorr 1982 and Gibson and Ezzi 1985). The general conclusion drawn from these studies is that planktivores can have a marked impact upon their prey communities. Durbin and Durbin (1975) suggested that the large biomass of nannoplankton in Narragansett Bay was due to the selective removal of the larger particles by the menhaden, *Brevoortia tyrannus*, and the stimulation of the remaining smaller phytoplankters by the fishes' excretory products. Hunter and Dorr (1982) argued that the Northern anchovy, *Engraulis mordax*, may regulate its own population size through

cannibalism due to selective filter feeding on its eggs. This effect of grazing activity has been demonstrated in the field for both fresh water (Warshaw 1972; Drenner and De Noyelles 1982) and marine (Koslow 1981) environments.

The present study was initiated to:

A. obtain feeding rates of *E. capensis* upon different sized food particles essential for future energy budget work,

B. confirm and elaborate upon the findings of an earlier field study (Chapter two) and

C. investigate the selective feeding behaviour displayed by the Cape anchovy.

METHODS AND MATERIALS

Schools of 19 - 48 wild anchovy, mean length 100.4 ± 5.86mm, were maintained in a 3 m or 2 m diameter tank supplied with a continuous flow of 5 µm filtered seawater at ambient temperature (16°-18°C). The size of the schools varied due to mortality and sacrifices for other experiments. The tanks were restocked 6 times during the 2 year experimental period using the technique of James (Chapter three).

The 3 m tank was in a laboratory illuminated by a 150 W incandescent bulb on a 12 hour light / 12 hour dark cycle. The 2 m tank

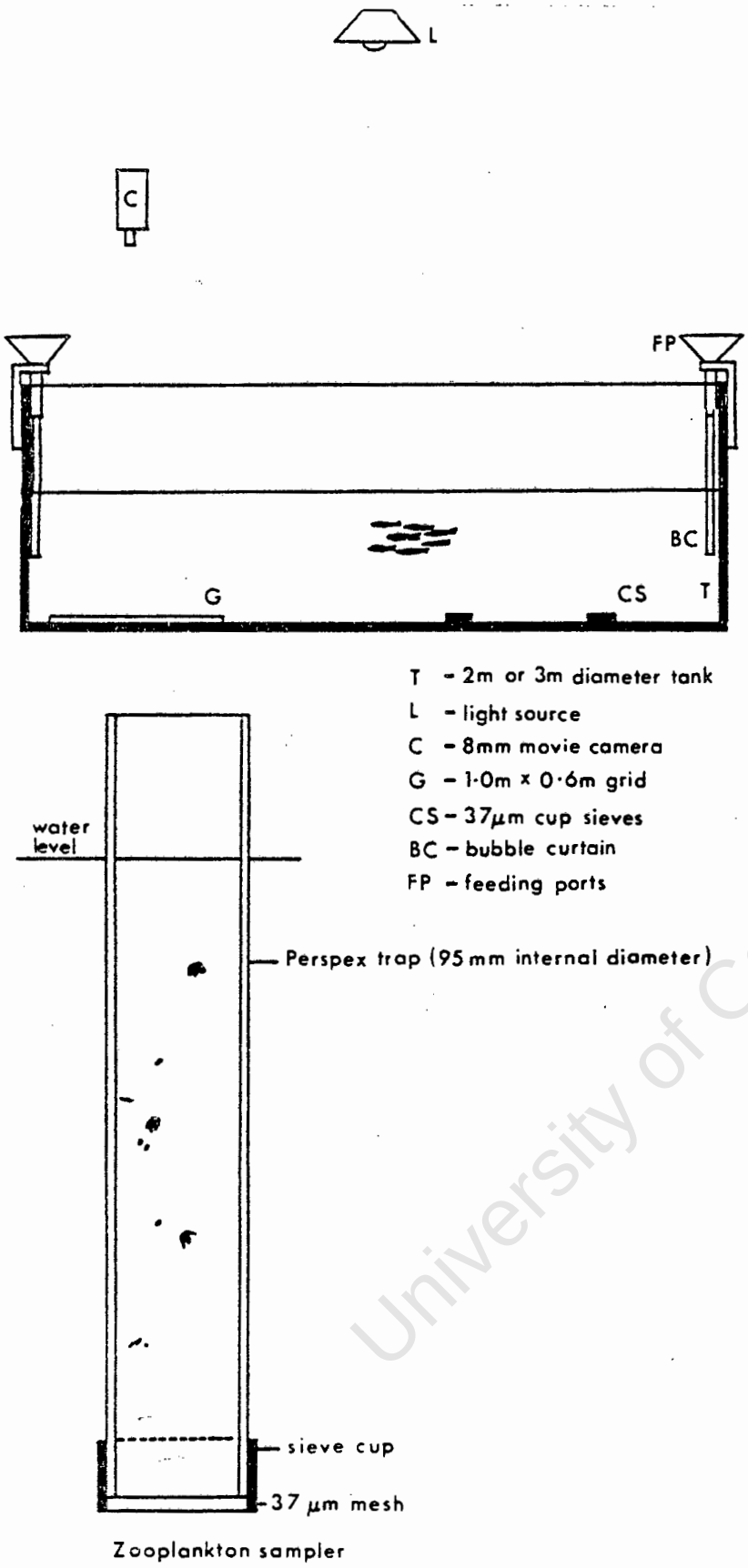


FIGURE ONE : Diagram of experimental apparatus used to investigate the feeding behaviour of the Cape anchovy

was in an outside working area covered by 55% shadecloth and was subject to the natural diurnal cycle. Both tanks had a porous airline around the circumference which produced a continuous fine bubble curtain up the sides (Fig. 1). Preliminary tests, without fish, using *Artemia salina* nauplii indicated that this bubble curtain effectively mixed the tanks and maintained a uniform prey distribution for the duration of the experiments (up to 5 hours).

The fish were fed dry trout pellets, a beef liver, anchovy or rock lobster offal mixture (see appendix B), frozen zooplankton and occasionally live *A. salina* and wild zooplankton when available.

All the food types used in the experiments were reared in the Institute's culture facility. The phytoplankters used were *Chaetoceros* spp., a chain forming genus, and the solitary pennate, *Thallasionema* sp.. The zooplankters were *A. salina* cysts, nauplii, juveniles and adults, the calanoid copepods *Paracartia africana*, *Paracalanus* scotti, *Calanoides carinatus* and *Pseudodiaptomus hessi*, and the rotifers *Brachionus plicatilis* and *Synchaeta* spp. Wild *Talorchestia capensis* and *Euphausia lucens* were maintained in the culture facility for use in one experiment. The diatoms ranged in size from 0.0114 mm - 0.1140 mm and the zooplankton from 0.129 mm - 16.422 mm. The phytoplankton was cultured in 5l - 300l batches and the zooplankton in 200l - 2500l containers, depending upon the volume required. All water used for culturing was filtered through 0.45 µm millepore filters.

TABLE 1: Summary of the information collected for each of the experimental feeding trials.

EXP. No.	No.OF FISH	TANK DIA m	TANK VOL.	INITIAL TIME hrs.	LIGHT LEVEL	STARVATION TIME hrs	FOOD TYPE	FOOD SIZE mm	METHOD OF MEASURING SWIMMING SPEED	FOOD DRY WT	FOOD C/N	FAECAL ELIMIN-ATION RATE	FAECES C/N	N EXCRETION RATE
2	46	3.0	3535	10.00	LIGHT	24	*C.carinatus*	2.490	STOPWATCH	+	-	-	-	-
3A	"	"	"	"	"	"	*P.africana*	1.160	"	+	-	-	-	-
B							*C. carinatus*	2.285						
4	"	"	"	"	"	"	*A. salina*	0.411	"	+	-	-	-	-
5	"	"	"	"	"	"	*A. salina*	0.530	"	+	-	-	-	-
6	"	"	"	"	"	"	*P. hessi*	0.910	"	+	-	-	-	-
7A	"	"	"	"	"	"	*A. salina*	0.600	"	+	-	-	-	-
B							*A. salina*	0.510						
8	"	"	"	"	LIGHT/ DARK	12	*A. salina*	0.448	"	+	-	-	-	-
9	"	"	"	12.00	LIGHT	24	*A. salina*	7.110	"	+	-	-	-	-
10	"	"	"	"	DARK	"	*A. salina*	7.732	"	+	-	-	-	-
11	"	"	"	10.00	"	"	*A. salina*	0.540	-	+	+	-	-	-
12	45	"	"	"	LIGHT	6	*A. salina*	0.541	STOPWATCH	+	-	-	-	-
13	41	"	"	"	"	24	*B. plicatilis*	0.256	"	+	+	-	-	-
14A	48	2.0	1570	09.00	"	"	*A. salina*	0.740	"	+	+	-	-	-
B							*A. salina*	0.902						
C							*A. salina*	1.105						
D							*A. salina*	1.413						
15A	30	2.0	1005	"	"	36	*Synchaeta* sp.	0.129	FILM	+	+	+	+	+
B							*A. salina*	0.544						
C							cysts	0.224						
16A	"	"	911	"	"	"	*A. salina*	0.711	"	+	+	+	+	+
B							cysts	0.225						
17A	29	"	958	"	"	"	*Chaetoceros*	0.093	"	+	+	+	+	+
B							*Thallassionema*	0.040						
18A	"	"	707	"	"	"	*A. salina*	0.725	"	+	+	+	+	+
B							*A. salina*	0.893						
C							*A. salina*	1.071						
D							*A. salina*	1.261						
E							cysts	0.226						
F							*P. crassi-rostris*	0.484						
19A-J	19	"	613	"	"	"	*Chaetoceros* 1 - 10 cell chains	0.011 - 0.114	"	+	+	+	+	+

Before an experiment the fish were starved for 6 - 36 hours. The sides and bottom of the tanks were thoroughly scrubbed and vacuumed the day before to remove attached growth. This procedure was repeated 2 - 3 hours before the start of the experiment and the tank flushed with filtered seawater. The 5 µm filter effectively removed any potential food particles from the seawater. Just before the start, the water supply was cut off and the tank lowered to a suitable level, depending on the number of fish in the tank and the density of food required (Table 1).

The food was introduced to the tank through 4 feeding ports (Fig. 1). The bubble curtain ensured thorough mixing within 1 - 2 mins. of introduction. The fish settled down and started to feed within 5 mins. of the addition of the food to the tank. The experiment was considered to have commenced (T=0) when the majority of the fish had begun feeding.

Plankton samples were taken at T=0 and at appropriate intervals thereafter until feeding ceased.Two different sampling methods were used; phytoplankton was sampled by collecting 5 x 100 ml aliquots with a syringe randomly throughout the tank at each time interval. The samples were preserved in 4% formalin and later the chains of different length were enumerated according to Utermohl as described by Hasle (1978). Cell dimensions were measured to calculate cell volume and modified Strathman equations (Parsons

et al 1984) were employed to convert cell volume to carbon content. Pre-experimental samples were used to determine the carbon, nitrogen and energy contents of the phytoplankton in several experiments (Table 1). Zooplankton sampling employed a perspex tube (95 mm internal diameter) which mated with 37 µm mesh cups spread randomly across the bottom of the tank (Fig. 1). After mating the combination was withdrawn from the tank, concentrating the zooplankton on the mesh. There were 3 advantages in using this method over methods cited in the literature:

A. placing the perspex tube in the tank did not disturb the fish, it being virtually invisible in the water,

B. the sample was integrated over the entire water column with little chance of the zooplankton avoiding the tube as they would a siphon, and

C. the tank volume did not change during the course of the experiment.

Three to five samples were taken at each time interval and preserved in 4% formalin for subsequent measuring and counting using a dissecting microscope. Pre-experimental samples of the food were collected , measured, counted and dried at 60°C for 24 hours to obtain a mean dry weight/ individual for each size class of prey offered as food. The experimental samples were then converted to µg dry weight/l accordingly. In several cases (Table 1) pre-experimental samples were further examined to obtain carbon, nitrogen and energy contents of the food.

Continual observations of schooling behaviour and swimming speed were made before and during each experiment. Swimming speed was measured with either a stopwatch or by using a 1.0 m * 0.6 m grid marked in 0.1 m squares and a 8 mm movie camera at 18 frames/s, in which case the fish were filmed for a total of 10 - 15s as they passed over the grid (Table 1). Changes in the direction executed by the fish, defined as a deviation of more than 20° from the direction of motion recorded during the previous 6 film frames (1/3 sec.) were recorded and used to measure the turning rate (turns/fish/min.) of the fish during feeding. Experiments were aborted if fish did not feed or displayed schooling behaviour inconsistent with the norm established during preliminary work. Experiments were terminated when all the fish had ceased to feed.

To investigate the levels of food required to initiate feeding of a school, small aliquots of prey were introduced to the tank sequentially at 3 - 5 min. intervals, with subsequent samples collected for enumeration, until at least 50% of the school was observed to be feeding. This exercise was carried out either before the start of a feeding trial (Exps. 13 and 19) or constituted a separate experiment (Exp. 11).

Reactive distances (Holling 1966) of the anchovy to prey were measured by placing 1 - 2 prey in 1l of water which was introduced

to the tank at varing distances from the fish by means of a funnel and a submerged pipe. Film was used to record behaviour and measure the reactive distance. Each prey type was offered on 15 separate occasions.

RESULTS

Feeding Behaviour

The anchovy employs the burst and glide swimming technique described by Leong and O'Connell (1969) for *Engraulis mordax,* consisting of a series of 4 - 5 tailbeats followed by a glide. When accelerating the number of tailbeats may increase to as many as 10. Changes in direction are usually executed at the beginning or end of the burst period. The swimming behaviour of the fish was not affected by the presence of observers either during feeding or when food was absent, provided that sudden movements around the tank were avoided. The fish were most excitable when food was absent or depleted at the end of a trial.

In the absence of food *Engraulis capensis* schooled in the midwater of the tank, the schools tending to be twice as long as they were broad. The fish appeared to maintain a stable position within the

school and individuals executed few independent changes in direction. If a current was generated in the tank the fish generally swam against it during the day and whilst feeding and with it at night. Individual fish would occasionally "gape" - opening their mouths wide and flaring the opercula for 0.2 - 1.0 sec. - in the absence of food. This gaping reduced the fish's swimming speed, neccessitating an acceleration to catch up with the school. Only 2 - 3 fish would gape at any one time. The swimming speed of undisturbed fish ranged between 0.73 BL/s and 1.88 BL/s, mean for all experiments of 1.695 ±0.591 BLS . The lower and higher speeds recorded were due to the decelerations and accelerations associated with gaping behaviour.

The feeding mode employed by *E. capensis* depended primarily upon food type and size. Phytoplankton and microzooplankton (< 0.710 mm) elicited filter and larger zooplankton particulate - feeding behaviour.The fish generally fed in the midwater, but observations during preliminary work demonstrated that *E. capensis* was capable of obtaining prey both from the bottom of the tank and the water's surface. These two feeding modes will be described before considering the more usual midwater feeding. No attempts were made to quantify the feeding rates of these two modes.

When attacking gammarid amphipods on the bottom, the fish moved towards the bottom at an angle of about 30° from the vertical after locating the prey - which may have remained unnoticed for

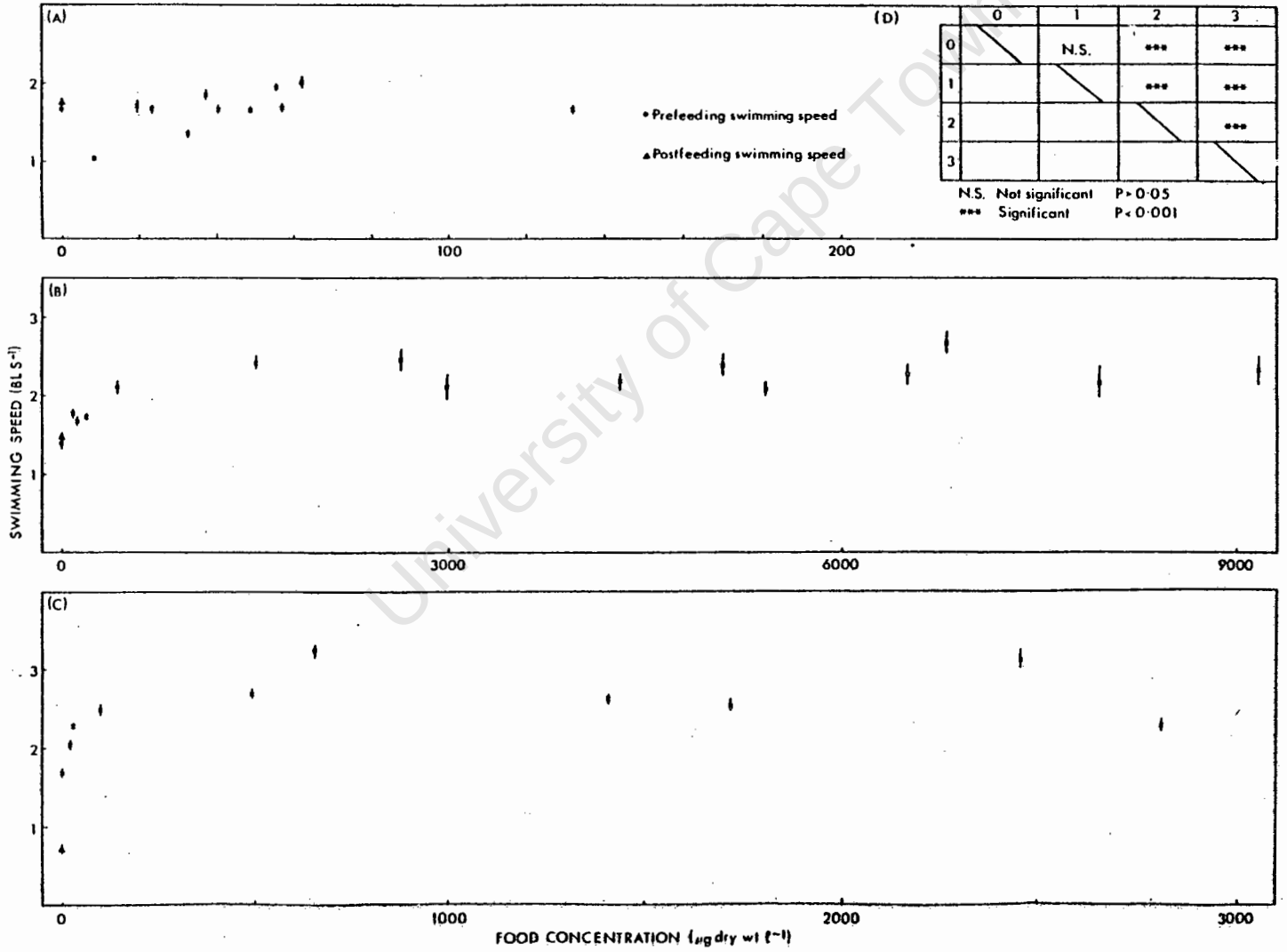
some time - and struck at it several times in rapid succession. After an attack the fish rose 5 - 10 cm off the bottom and began searching for more prey. Following several successful strikes the fish remained closer to the bottom (2 - 3 cm) at an angle of 20° - 40° from the vertical searching for and attacking prey items. Usually only a few individuals would respond to bottom dwelling prey whilst the rest of the school remained in midwater, although on several occasions entire schools were observed feeding in this manner.

Surface feeding occurred more frequently than bottom feeding and, unlike the latter, if one fish initiated the behaviour, the rest of the school rapidly followed suit. The fish approached the prey (*Talorchestia capensis*, an amphipod) rapidly at a steep angle, rolling on to their flanks upon reaching the target, breaking the surface with the head and flank as the prey were captured. The fish then turned sharply and, powered by strong tail beats, headed down to midwater before turning to make another strike.

Filter Feeding

When phytoplankton or microzooplankton were introduced to the tank the fish began to gape frequently - as if "tasting" the water, similar to the behaviour described by Durbin and Durbin (1975) for *B. tyrannus*. If the concentration of food was below some threshold level this gaping soon ceased, but if above then

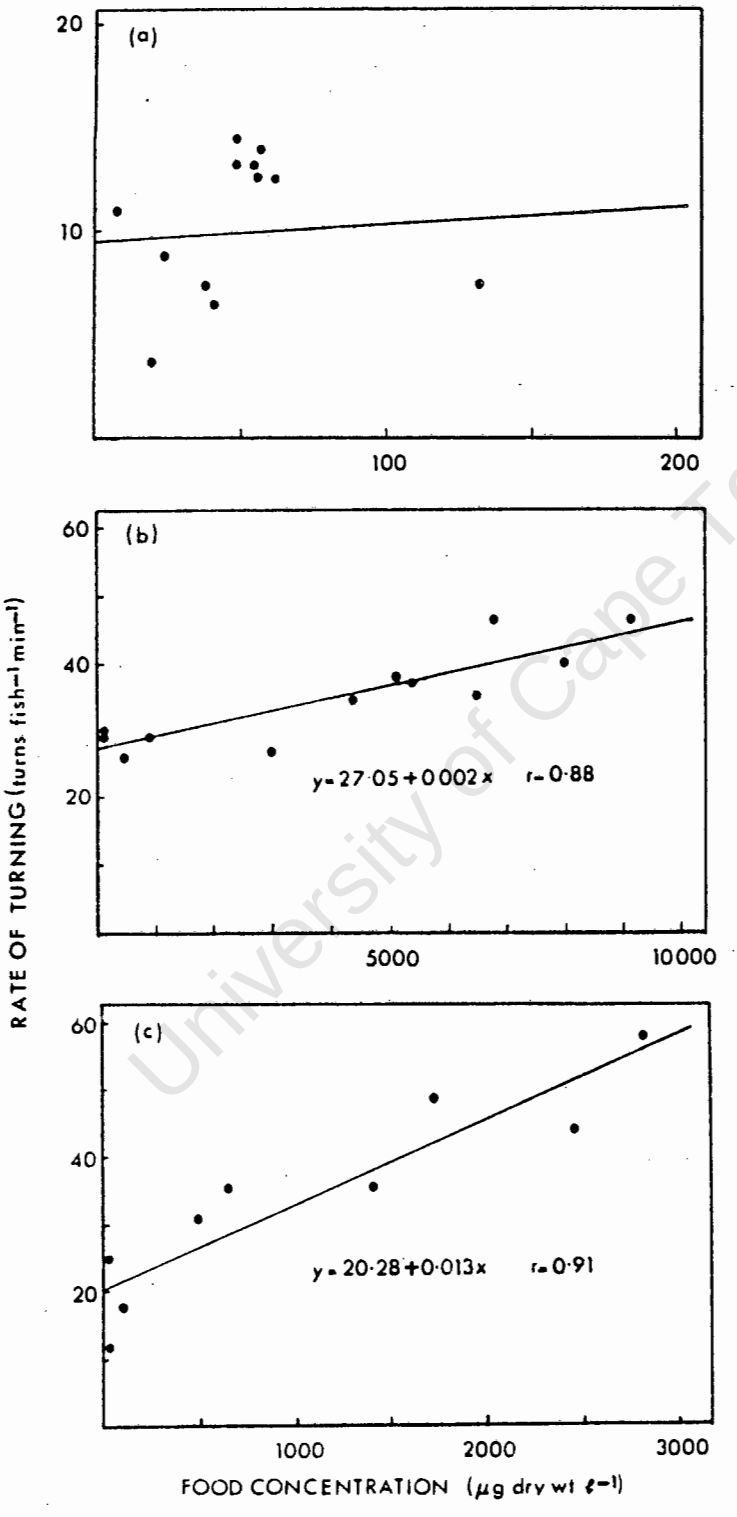
FIGURE TWO : Swimming speeds of feeding anchovy as a function of food concentration. A) Filter feeding upon Chaetoceros sp. 1-10 cell chains (Exp. 19). B) Filter feeding upon A. salina nauplii and cysts (Exp. 16). C) Particulate feeding upon A. salina juveniles. (Exp. 18). The bars indicate the 95% confidence limits. D) Results of F tests comparing the differences in swimming speeds of non-feeding fish (0) and fish feeding upon (1) phytoplankton, (2) microzooplankton and (3) mesozooplankton. Only experiments during which film was used to record behaviour have been analysed.



the school readily started to filter feed. A filtering bout commenced with the mouth opening wide, the protrusion of the lower jaw and the opercula flaring. When observed from above the head was tulip - shaped as described by Gibson and Ezzi (1985) for filter feeding *C.harengus*. As the mouth opened the tail beat strongly at a greater amplitude than during undisturbed swimming. Filtering continued for 0.4 - 3.0 s and 3 - 12 tail beats accompanied each bout. The mouth closed just before the end of the last tail beat and a short glide followed. Changes in direction during filtering occurred at the beginning or end of the glide; rarely during an actual filtering bout. The fish schooled more densely while filtering and the shape of the school changed so that it was approximately 1.5 to 2 times as broad as it was long. The feeding school moved throughout the water column, though never approaching closer than 8 - 10 cm of the bottom.

When feeding upon *Chaetoceros* sp. the swimming speed was not significantly different from the non-feeding speeds (1.632 ± 0.491 BL/s Fig 2A). The mean turning rate during filtering upon phytoplankton was not significantly different from the non - feeding turning rate ($F=0.49$ $P>0.05$), nor was there a correlation between the rate of turning and the concentration of food in the tank, the slope not being significantly different from zero ($F=0.1$ $P>0.05$; Fig.3A), implying that there was no orientation towards the food particles present in the water. The only discernable differences between the undisturbed state and feeding upon

FIGURE THREE : The rate of turning anchovy as a function of food concentration. (a) Filter feeding upon Chaetoceros sp. 1-10 cell chains (Exp. 19). (b) Filter feeding upon A. salina nauplii and cysts (Exp. 16) (c) Particulate feeding upon A. salina juveniles (Exp. 18).



phytoplankton were the short filtering bouts and the altered density and shape of the school.

During filter feeding upon microzooplankton the swimming speed differed significantly from the undisturbed values (2.060 ±0.826 BL/s Fig. 2B). There was a significant correlation between the rate of turning and the food concentration ($F=35.2$ $P<0.05$; Fig.3B), indicating that the fish orientated themselves towards food particles to some degree. This suggestion is supported by observations during preliminary experiments when patches of food developed in the tanks due to inadequate mixing.The fish concentrated their feeding activity in the areas of high food density, making sharp turns to maintain themselves in these regions. Similar activity was noted when water which had contained zooplankton or washings of frozen zooplankton were introduced to the tank. The fish moved to the area of the tainted water gaping frequently before losing interest. This behaviour further indicates that there may be a chemical cue to trigger filter feeding, but that the presence of particles- possibly sensed by mechanoreceptors on the gillrakers - are required to stimulate its continuation. The elevated swimming speeds remained constant over a wide range of food concentrations, although there was considerable variation around the mean (Fig.2B). The glides appeared to be shorter and the filtering bouts longer and more frequent when the food was zooplankton, but the poor resolution of the film precluded any accurate measurements of the duration and frequency of mouth

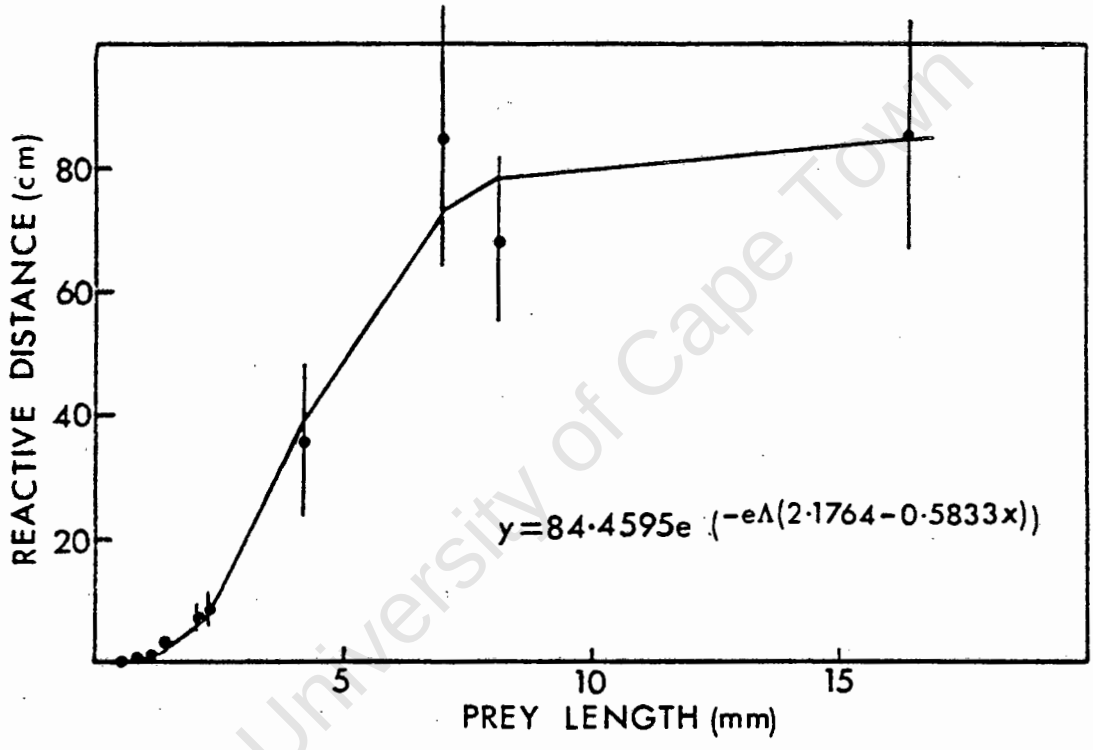
opening during the experiments. A sudden change in light intensity during one trial (Exp.8) due to a power failure indicated that light intensity had no effect on schooling and feeding behaviour. The clearance rate obtained from this trial was similar to those of trials conducted in light con- ditions with the same food type. This result is similar to that of Holanov and Tash (1978) for *Dorosoma petenense*.

Particulate Feeding

Schooling broke down immediately after the initiation of particulate feeding with the fish continually changing direction independently to attack prey. The entire tank was covered by the fish during the initial explosion of feeding activity which was similar to the feeding frenzy described by Leong and O'Connell (1969) for *E. mordax* and Durbin and Durbin (1975) for *B. tyrannus*. After 5 - 10 minutes the fish formed a loose aggregation which moved rapidly around the tank. The fish still acted independently within this loose structure, turning frequently and attacking prey as encountered. This behaviour was modified towards the end of a trial when the fish began to school more cohesively, but the swimming speed remained elevated and feeding continued.

Swimming behaviour was strongly modified during particulate feeding, being characterised by almost continual large amplitude tail beats interspersed with sporadic, very short glides which preceded

FIGURE FOUR : Reactive distances of 10.04cm Cape anchovy as a function of prey length. Each point is the mean of 15 seperate estimates; the bars indicate the 95% confidence limits.



strikes at prey. During a biting attack the mouth started to open as the glide commenced and the prey seemed to be sucked into the mouth with the surrounding water and swallowed whole; the water exiting through the opercula, which were slightly flared after prey capture. The lower jaw was not protruded as during filter feeding. The length of the glide and the behaviour immediately prior to the act of capture depended on prey size. The duration of the glide and mouth opening were shorter for smaller items (0.72 mm - 3.00 mm) than for larger ones (7.00 mm +). The classic S - shaped strike posture was only assumed by fish attacking large prey, such as adult *Euphausia lucens* . Leong and O'Connell (1969) found that the glide eliminated lateral head movement during the crucial orientation period immediately before the fish attacked its prey.

Biting was characterised by swimming speeds that were significantly greater than those recorded for both the undisturbed and the filter feeding states (2.412 ±0.700 BL/s Fig. 2C). As during filtering, the elevated swimming speeds were independent of the concentration of food in the water, showing considerable variation around the mean values (Fig. 2C). The numerous turns, which were closely correlated to the concentration of food ($F=34.9$ $P<0.05$; Fig. 3C) and appeared to be primarily concerned with orientation towards prey items, were all executed before the start of the glide. There was a significantly higher degree of orientation during particulate than during filter feeding ($t_{æ(2)}19$, 4.05

TABLE 2: Reaction distances of 100.4 mm anchovy to various sizes of prey. Each prey type was offered on 15 separate occaisions.

PREY TYPE	PREY SIZE mm	REACTION DISTANCE cm RANGE	MEAN	S.D.
A. salina nauplii	0.530	-	-	-
A. salina juveniles	0.780	0 - 2.3	0.55	0.66
	1.108	0 - 2.5	1.01	0.87
	1.347	0.8 - 6.7	3.28	1.80
	2.030	3.3 - 13.6	7.63	3.20
A. salina adults	7.014	25.0 - 153.0	84.73	40.81
	8.100	19.1 - 104.5	68.11	25.45
C. carinatus	2.260	1.6 - 18.4	8.63	5.49
P. hessi	1.106	0 - 1.7	0.63	0.64
Talorchestia capensis	4.205	0 - 75.0	35.60	23.49 *
Euphausia lucens	16.422	37.0 - 200.0	85.07	37.02

* Prey floated on the waters' surface.

TABLE 3: Volumes searched by 10.04 cm anchovy for the prey sizes offered during the biting trials.

PARTICLE SIZE mm	EXPECTED REACTIVE DISTANCE cm	REACTIVE AREA m²	SWIMMING SPEED cm/s	VOLUME SEARCHED (Fmax) l/fish/min
0.910	0.474	7.058e-5	26.907	1.14
1.160	8.262	0.0214	29.437	378.76
2.285	8.262	0.0214		
2.490	10.736	0.0362	25.900	562.71
0.740	*1.769	9.831e-4	28.092	16.57
	#0.827	2.149e-4		3.62
0.902	*1.769			
	#0.827			
1.105#	*1.769			
	#0.827			
1.413*	*1.769			
0.725	+1.236	4.800e-4	24.216	6.97
	@0.753	1.781e-4		2.59
0.893	+1.236			
	@0.753			
1.071@	+1.236			
	@0.753			
1.261+	+1.236			
7.110	73.474	1.696	31.13	31677.26
7.732	76.656	1.846	32.89	36429.84

* reactive distance when largest particle is 1.413mm
# " " " " " " 1.105mm
+ " " " " " " 1.261mm

$P<0.001$ Fig. 3C). However, no differences in feeding behaviour were observed between light (Exp. 9) and dark (Exp. 10) trials using the same food type. Indeed, the clearance rate was greater during the dark experiment. This suggests that *E. capensis* either has extremely acute vision or that another sensory organ, such as the lateral line, plays an important role in prey location.

Table 2 and Fig. 4 present data concerning the distance over which *E. capensis* can detect and will react to the presence of differing sizes of prey. For larger particles this distance may be considerable - up to 10 body lengths. It was noted that the reactive distance tended to increase if the same prey type was offered on many consecutive occasions; therefore the different prey items were offered in a random order to avoid this. These data were difficult to quantify and can only be considered as rough estimates of reaction distances. However, they are important as they provide insight into the maximum volume that an anchovy is capable of searching during particulate feeding (Table 3). The results show that prey size is a primary factor influencing prey location and orientation of the fish during biting and that there is a threshold size (± 8.00mm) above which reactive distance is independent of prey size.

FIGURE FIVE : The concentration of food required to initiate filter feeding by Cape anchovy as a function of prey size.

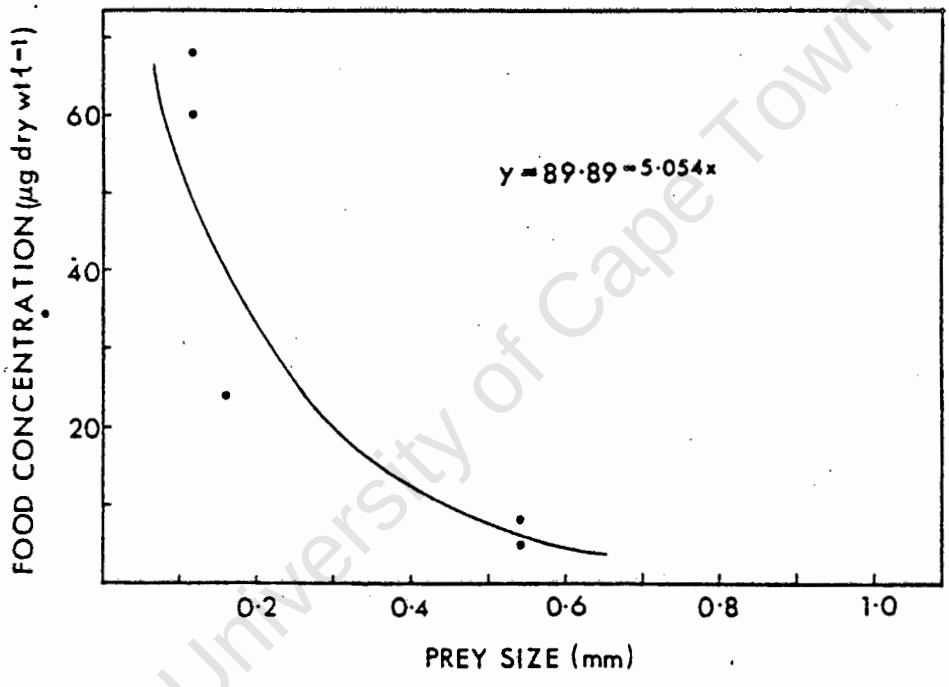


TABLE 4: Levels of food required to initiate filter feeding.

EXP. No.	PREY TYPE	PREY SIZE mm	No/l	DRY WT./l µg/l	µg C/l	
11	*A. salina* nauplii	0.540	4.5	5.10	0.96	
			4.5	5.10	0.96	
			7.2	8.20	1.55	
13	*B. plicatilis*	0.158	56.1	24.10	8.37	*
19	*Chaetoceros* sp.	0.011 - 0.114	506705.0 - 574001.0	59.87 - 67.85	18.62 - 21.10	*

* Estimates made before the start of the main experiment.

Initiation of Feeding

Very low threshold concentrations were required to initiate particulate feeding upon larger prey (> ± 0.720 mm) during the experiments - the fish attacked even single prey items introduced to the tank (1 copepod/3.55m³), making large deviations from their original path to capture the item (Fig. 4). Threshold concentrations were, however, necessary to initiate filter feeding upon smaller items (< ± 0.710 mm; Table 4). The data indicate that threshold concentrations, in terms of numbers and biomass, were inversely related to prey size (Fig.5). Durbin and Durbin (1975) drew similar conclusions for *B. tyrannus*, but Hunter and Dorr (1982), who investigated threshold concentrations required to initiate filtering in *E. mordax*, found that although the density threshold was negatively correlated to prey size, that for biomass was positively correlated to size.

Termination of Feeding

E. capensis terminated filter feeding at levels considerably below those required for its initiation (Table 5). The threshold concentrations for a wide range of prey were similar and appeared to be independent of particle size. Four trials, using *A. salina* cysts (Exps. 15C and 16B), *Synchaeta* spp. (15A) and *Chaetoceros* and *Thallassionema* spp. (Exp. 17A,B) as food produced elevated

TABLE 5: Concentrations of food in the tank at the termination of feeding.

FEEDING MODE	EXP No.	PREY TYPE	PREY SIZE mm	No/l	DRY WT./l µg/l	µgC/l	
FILTERING	4	*A. salina*	0.411	3.5	3.0	-	
	5	"	0.530	1.3	2.0	-	
	7A	"	0.600	3.2	7.0	-	
	B	"	0.510	2.0	3.0	-	
	8	"	0.448	3.1	4.0	-	
	11	"	0.540	0.6	0.7	-	
				1.0	1.3		
	12	"	0.541	0.4	1.0	-	
	13	*B. plicatilis*	0.256	48.4	21.0	7.30	
	15A	*Synchaeta* sp.	0.129	555.5	-	-	*
	B	*A. salina*	0.544	3.1	5.0	0.94	
	C	cysts	0.224	68.0	102.0	43.35	
	16A	*A. salina*	0.711	3.9	11.0	2.09	
	B	cysts	0.225	59.9	90.0	36.91	
	17A	*Chaetoceros* sp.	0.093	1483280	80.3	24.9	*
	B	*Thallassionema* sp.	0.040	1597860	509.6	160.0	*
	18E	*A. salina* cysts	0.226	1.9	3.0	1.28	
	F	*Paracalanus* sp.	0.484	0.6	2.0	0.24	
	19I	*Chaetoceros* sp.	0.103	37503	4.68	1.38	
	J	"	0.114	31524	3.93	1.16	
BITING	2	*C. carinatus*	2.490	0	0	-	
	3A	*P. africana*	1.160	0.3	11.0	-	
	B	*C. carinatus*	2.285	0	0	-	
	6	*P. hessi*	0.910	0.3	11.0	-	
	9	A. *salina*	7.110	0	0	-	
	10	"	7.732	0	0	-	
	14A	"	0.740	2.1	7.0	1.32	
	B	"	0.902	1.0	5.0	0.94	
	C	"	1.105	0	0	-	
	D	"	1.413	0	0	-	
	18A	"	0.725	4.3	14.0	2.64	
	B	"	0.893	2.7	12.0	2.27	
	C	"	1.071	0	0	-	
	D	"	1.261	0	0	-	

* *E. capensis* was unable to significantly reduce the available concentrations of these food types during the course of the experiments.

terminal concentrations (Table 5). In the former experiments, these high values were possibly due to the cysts being unsuitable food and feeding activity ceased when the suitable prey had been depleted. The low value for cysts obtained from Exp. 18e was due to the fact that feeding continued at very low food densities during this experiment, the cysts being ingested accidentally as the fish pursued their preferred, but relatively scarce, prey. In no instance did the anchovy feed upon the cysts alone after the removal of the other prey types. In the latter cases, the fish displayed feeding behaviour, but with a lower incidence of filtering than was expected and the fish did not significantly reduce the food concentrations during the trials.

Termination of filter feeding upon zooplankton was marked by a rapid return to non - feeding behaviour, with 2 - 5 minutes elapsing between the first noticeable signs of a reduction in activity and its complete cessation. There was no such definite termination when phytoplankton was the food, when the incidence of filtering slowly declined and the shape of the school gradually reverted to the undisturbed configuration until non - feeding behaviour predominated.

During particulate feeding upon particles > 1.20 mm feeding activity was only terminated after all the food had been removed from the tank (Table 5). When prey between 0.720 mm and 1.20 mm were present feeding apparently ceased at concentrations between

5 and 14 µg dry weight/l (0.3 - 4.3 particles/l) - biomass values that were generally higher than those recorded for filtering upon smaller prey. These terminal concentrations are interesting since they exceeded the threshold concentrations required to initiate biting. There are two possible explanations for these unexpected results:

A. factors other than prey size, such as state of hunger, have a major influence on termination of feeding activity. Or, more likely;

B. the short reactive distances due to the small size of the prey, caused a reduction in the predator - prey encounter rate and hence feeding activity fell to such low levels that the observers terminated the trials prematurely. The fish probably cleared the remaining food from the tank at a low rate after the termination of the trial.

In the closing stages of a biting trial the predator strike rate did decrease rapidly and the fish began to school more cohesively, although individual fish still attacked prey and their swimming speed remained elevated. The transformation from the feeding to the non - feeding states was gradual, with the fish continuing to react individually to prey items as encountered, even when schooling behaviour resembled the non - feeding mode. This was especially so when small prey were present. It was, therefore, difficult to ascertain the true end point of these trials.

Feeding Rates

Feeding activity after the introduction of food to the tank invariably resulted in an exponential decline in the food concentration with time (Figs. 6-10), indicating that a constant proportion was removed per unit time during an experiment, regardless of the feeding mode or particle size. The slope of the semi-log plot is the mean "instantaneous feeding rate", g. The "clearance rate" (Strickler 1985) or the "volume swept clear per unit time", F (Harvey 1937, Frost 1972, Durbin and Durbin 1975), may be determined from the relationship:

$F = Vg/N$ where V = tank volume and N = no. of grazers

The term "clearance rate" will be adopted for this work rather than "the volume swept clear" per unit time, as the former makes no assumption about feeding behaviour while the latter implies filtering activity. The clearance rate, whether for biting or filtering, is an estimate of the volume from which all the food particles would have to be removed per unit time to produce the observed ingestion rates, I (Durbin and Durbin 1975; Marin *et al* 1986), where:

$I = [Ct]F$ and $[Ct]$ = food concentration at time t.

Following the reasoning of Durbin and Durbin (1975) all clearance rates have been expressed on a per fish rather than per gram basis.

FIGURE SIX : Cape anchovy filter feeding upon phytoplankton. (a) Chaetoceros sp. 11 cell chains and single Thalassionema cells. (b) Chaetoceros sp. 1-10 cell chains (0.0114-0.114mm). A - J represent the increase in chain length from 1 - 10 cells.

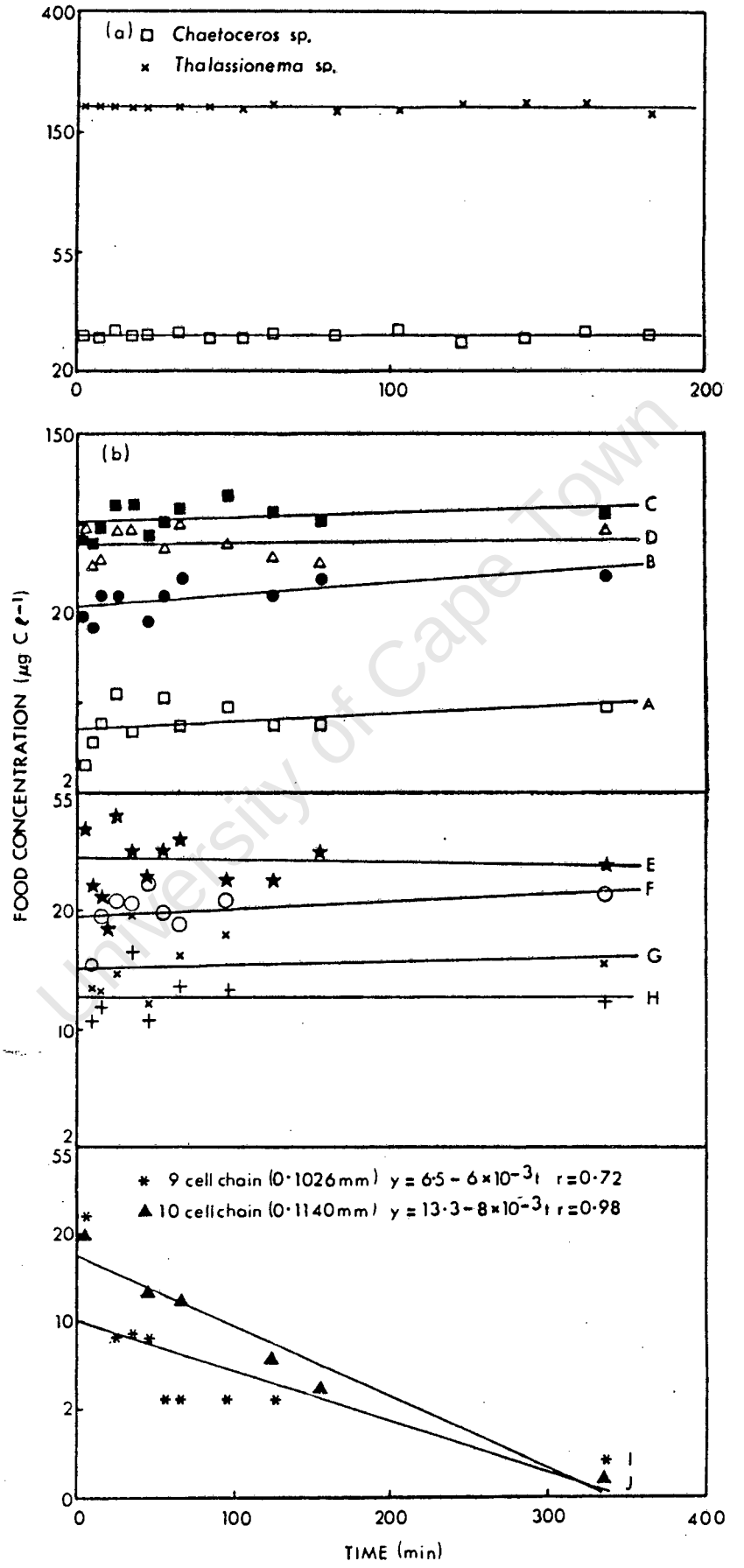


TABLE 6: Feeding rates of *Engraulis capensis* upon various sizes of prey. The standard deviations and 95% confidence limits are indicated for the swimming speeds (when film was used) and clearance rates (where the residual mean square > 0.1) respectively.

FEEDING MODE	EXP No.	PREY TYPE	PREY SIZE mm	MEAN SWIMMING SPEED BL/s	CLEARANCE RATE F l/fish/min	Fmax l/fish/min		F : Fmax %		Fmax+
FILTER FEEDING	17A	*Thallassionema*	*0.040*	*1.598* ± 0.330	-	2.305		-		
	17B	*Chaetoceros*	0.093		-			-		
	19A	*Chaetoceros*	0.0114	1.632 ± 0.491	-			-		
	B		0.0228		-			-		
	C		0.0342		-			-		
	D		0.0456		-			-		
	E		0.0570		-			-		
	F		0.0684		-			-		
	G		0.0798		-			-		
	H		0.0912		-			-		
	I		0.1026		0.194±0.112			8.42		
	J		0.1140		0.258±0.073			11.19		
	15A	*Synchaeta*	0.129	1.883	-			-		
	13	*B. plicatilis*	0.256	1.630	0.291			12.62		
	15C	*A.salina* cysts	0.224	2.100	0.402±0.082			17.44		
					(0.312)*			13.54		
	16B		0.225	2.059 ± 0.826	0.334			14.49		
					(0.264)*			11.45		
	18E		0.226	2.412 ± 0.670	0.926±0.082			40.17		
					(0.626)*			27.16		
	18F	*P. crassirostris*	0.484	2.412 ± 0.670	0.609±0.088			26.42		
					(0.495)#			21.48		
	4	*A. salina* nauplii	0.411	1.980	1.230±0.174			53.56		
	5		0.530	2.380	1.844±0.164			80.00		
	7A		0.600	2.500	2.305			100.00		
	B		0.510	1.980	1.844			80.00		
	8		0.448	1.860	1.383			60.00		
	12		0.541	1.950	2.278±0.145			96.70		
	15B		0.544	2.100	0.871±0.066			37.78		
	16A		0.711	2.059 ± 0.826	0.668±0.041			28.98		
BITING	6	*P. hessi*	0.910	2.680	2.920±0.519	0.114@		2561.40	17.7623	16.44
	3A	*P. africana*	1.160	2.932	0.692±0.215	37.876		1.83	"	3.90
	2	*C. carinatus*	2.490	2.580	14.140±1.076	56.271		25.13	"	82.08
	3B		2.285	2.932	22.055±6.839	37.876		58.23	"	124.17
	14A	*A. salina* juveniles	0.740	2.798	0.491	1.657		29.63	"	2.76
					3.009	0.362		831.22	"	16.94
	B		0.902		0.702	1.657		42.37	"	3.95
					4.841	0.362		1337.29	"	27.25
	C		1.105		1.341	1.657		80.93	"	7.55
					4.252±0.132	0.362		1174.59	"	23.94
	D		1.413		8.635±3.616	1.657		522.21	"	48.61
	18A		0.725	2.412 ± 0.670	0.439	0.698		62.89	"	2.47
					1.170±0.179	0.259		451.74	"	6.59
	B		0.893		0.780	0.698		111.75	"	4.39
					2.828±0.219	0.259		1091.89	"	15.92
	C		1.071		1.316	0.698		188.54	"	7.41
					4.218	0.259		1628.57	"	23.75
	D		1.261		7.801±2.901	0.698		1117.62	"	43.91
	9	*A. salina* adults	7.110	3.101	11.835±3.458	3168.140		0.37	"	66.63
	10		7.732	3.276	21.287±2.305	3643.100		0.58	"	119.84

* Clearance rates standardised against the swimming speeds recorded for *B. plicatilis* during Exp. 13.

\# Clearance rate standardised against the swimming speeds recorded for *A. salina* nauplii during Exp. 7B.

^ Fmax calculated from reactive distance data

Filter Feeding

The results of the two phytoplankton feeding trials are displayed in Table 6 and Fig.6. During Experiment 17 *E.capensis* removed neither the singe cells of *Thalassionema* (40 µm) nor the 11 cell chains of a *Chaetoceros* sp (93 µm) from the water, even though filtering activity persisted at a low level throughout the 3 hour trial period. When presented with a *Chaetoceros* sp monoculture containing 1 - 10 cell chains ranging in size from 11.4 - 114 µm (Exp.19), the fish, which displayed filter feeding activity throughout the 5.5 hour experiment, could not remove the 1 - 8 cell chains, but were able to filter the 9 and 10 cell chains at low rates (F = 0.194 l/fish/min and 0.258 l/fish/min respectively, Table 6; Fig. 6). These results indicate that the minimum size of particle filterable by anchovy is between 93.0 µm and 102.6 µm maximum dimension.

Filter feeding trials using monocultures of *A. salina* nauplii produced much greater clearance rates (Table 6; Fig. 7) which generally increased with increasing particle size. The initial concentration of food in the tank, which varied between 16.6 µg dry wt./l (Exp.7B) and 163.3 µg dry wt./l (Exp.12), had little effect on the feeding behaviour of the fish or the clearance rates. Prefeeding starvation times, which ranged from 6 - 36 hrs, also had no apparent effect on the clearance rates. During Exp.7, the fish were allowed to terminate feeding activity before more

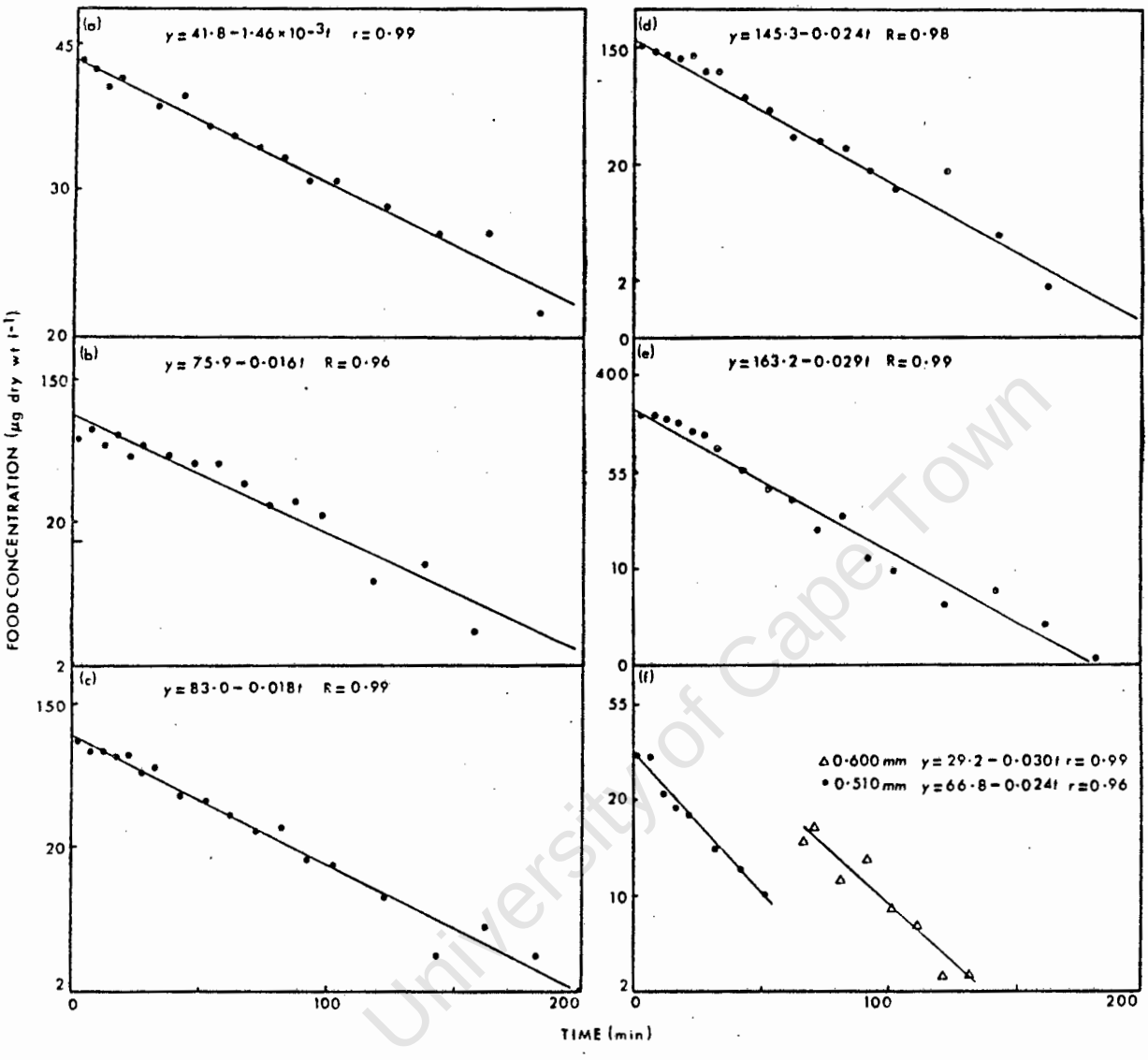


FIGURE SEVEN : Cape anchovy filter feeding upon monocultures of Brachionus plicatilis and Artemia salina. (a) Exp. 13 B. Plicatilis 0.256mm. (b) Exp. 4 A. salina 0.411mm. (c) Exp. 8 A. salina 0.541mm. (f) Exp. 7 A. salina 0.600mm and 0.510mm.

food was introduced to the tank.

There was considerable variation in the clearance rates obtained for *A. salina* nauplii between feeding trials, although within any one experiment variation was minimal (Table 6; Fig.7). Differences in particle size cannot account for these variations - the lowest clearance rate was obtained for the largest particle that the anchovy was observed to filter (Exp.16A). Variations in swimming speed and feeding behaviour, such as frequency and duration of filtering bouts, are the most likely causes of these variations. Visual observations substantiate this; eg., during Exp.16, the swimming speeds of the fish were similar to those recorded during other *A. salina* trials, but their feeding behaviour was abnormal, as the filtering bouts tended to be shorter and more sporadic than usual, with the fish also switching to particulate feeding for brief periods. Only detailed analyses of high quality video or film material, such as the work of Gibson and Ezzi (1985), would allow accurate assessment of the influence of these aspects of feeding behaviour upon the clearance rates of the anchovy.

At the start of Exp.15, the introduction of *Synchaeta* sp. initiated feeding behaviour, but the fish soon lost interest and terminated filter feeding after 25 minutes, without reducing the concentration of the rotifer in the water (Table 6; Fig.8). These results are interesting, as the fish, which were the same batch as those used in the phytoplankton trials (Exp.17 and 19), were apparently

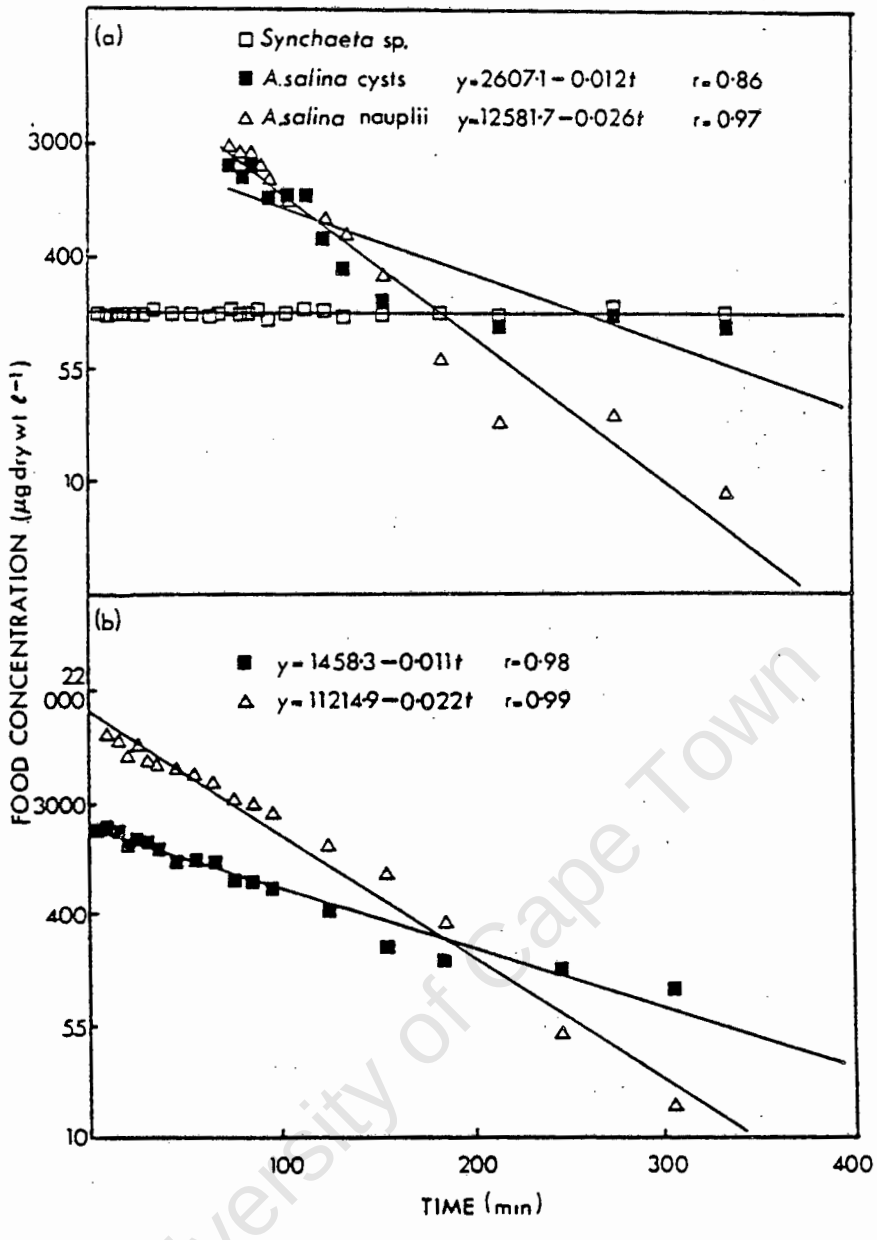
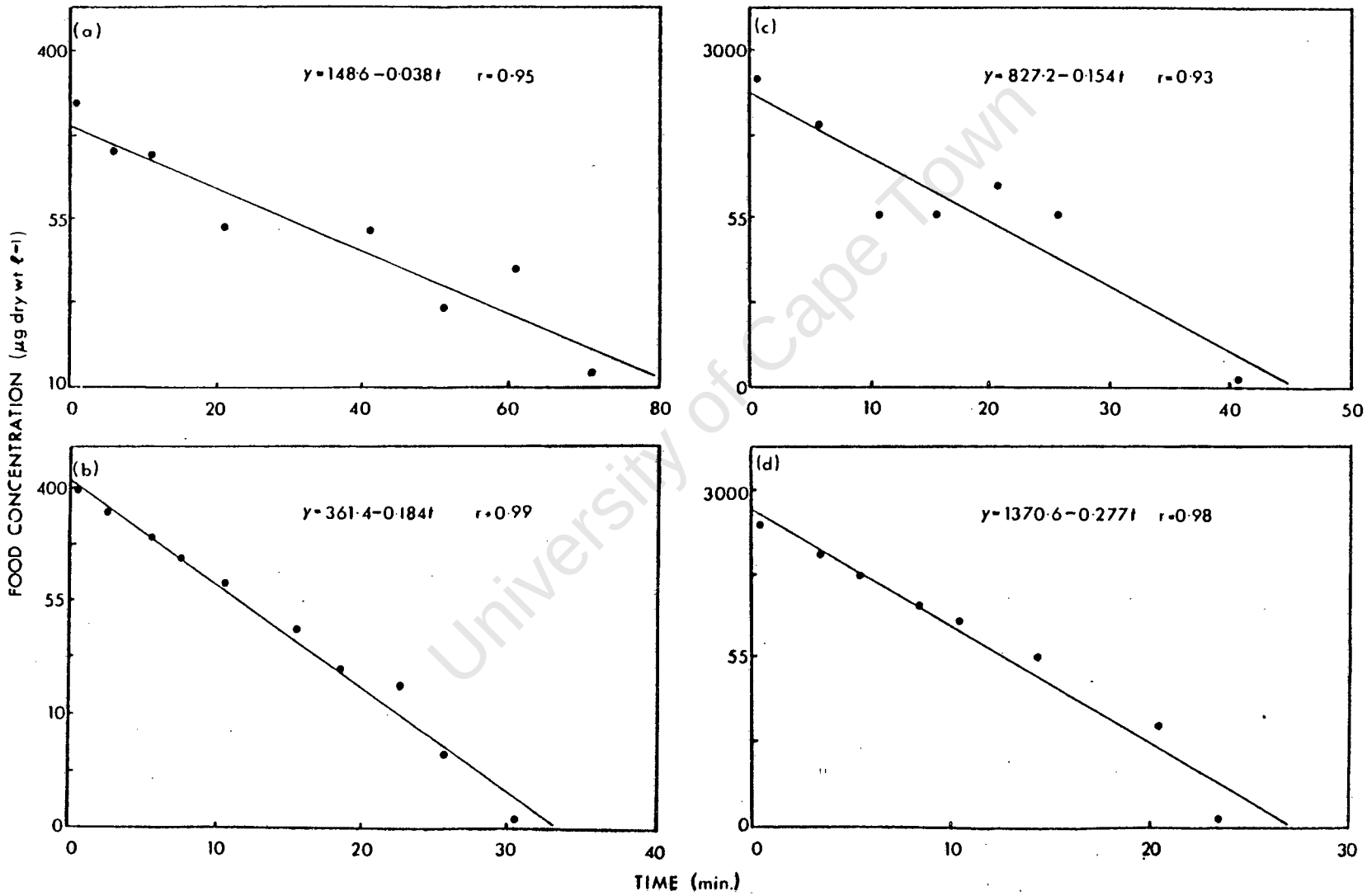


FIGURE EIGHT : Cape anchovy filter feeding upon mixed size assemblages of microzooplankton.

unable to remove particles above the minimum threshold size of 102.6 µm (9 cell chain of *Chaetoceros* sp, Exp.19i). Also, the fish ceased feeding upon the rotifer after 25 minutes without causing a reduction in its concentration, yet during Exp.17, the fish continued to attempt, unsuccessfully, to filter the phytoplankton from the water until the trial was terminated. The clearance rate obtained for *Brachionus plicatilis* (0.256mm, Table 5, Fig. 7) was only marginally greater than that for the 10 cell chains of *Chaetoceros* sp (114.0mm), although its measured maximum dimension was more than double that of the algae.

Three trials were carried out to determine the effect of mixed size assemblages of prey upon filter feeding clearance rates (Table 6; Fig.8 and 10). During two of the trials only filterable foods were presented to the fish (*A. salina* nauplii and cysts; Exps.15 and 16), while in the third, both biteable and filterable foods were available (*A salina* juveniles, cysts and *P. scotti*; Exp.18). In both the filter feeding trials, the clearance rates of the nauplii were considerably lower than during experiments using *A. salina* monocultures. The clearance rates for the cysts were greater than would be expected for a particle of that size - the clearance rate obtained for *B. plicatilis* was 0.291 l/fish/min compared to 0.334 l/fish/min and 0.4021/fish/min for the cysts (Table 6). The rate obtained for the cysts during the biting experiment was even greater (0.9261/ fish/min). These increased rates may be partially attributable to the faster swimming speeds

FIGURE NINE : Particulate feeding by Cape anchovy upon monocultures of mesozooplankton. (a) Exp. 6 P. hessi 0.910mm. (b) Exp. 2 C. carinatus 2.490mm. (c) Exp. 9 A salina 7.110mm. (d) Exp. 10 A. salina 7.732mm.



recorded during these trials relative to the speed recorded for the *B. plicatilis* trial. The cyst clearance rates from the filtering trials become very similar to that of *B. plicatilis* when standardised against the swimming speed recorded during the latter trial (Table 6). Durbin and Durbin (1975) made similar findings when mixed size assemblages of zooplankton and phytoplankton were presented to *B. tyrannus*. However, the cyst clearance rate obtained from the biting trial remains greater, even after standardisation, probably due to the different feeding mode. In contrast to the cyst clearance rate obtained from Exp.18, that for *P.* scotti was lower than expected, especially after standardisation. *P.* scotti is capable of burst swimming speeds equivalent to many BL/s which is its main escape response. It is possible that during this trial, in which the anchovy were not directing their feeding activity towards it, *P.* scotti avoided capture by using this escape response, thereby causing a reduction in the clearance rate relative to that obtained for the passive cysts.

Particulate Feeding

The results of the biting trials are shown in Table 6 and Figs. 9 and 10. As during filter feeding, the clearance rates increased with particle size, with little variation during an experiment, but considerable differences being noted between experiments, both when monocultures and mixed size assemblages of prey were offered to the fish.

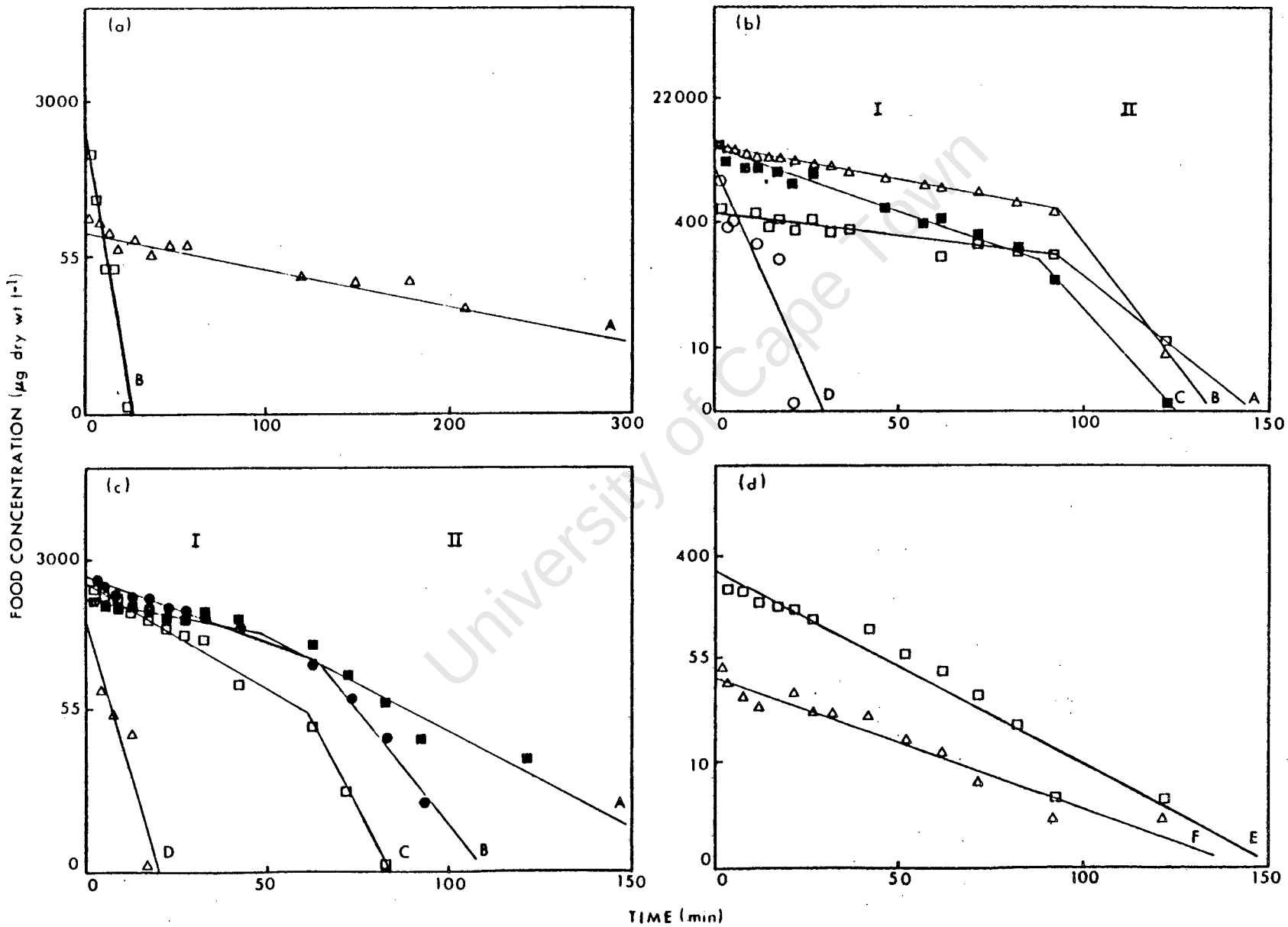


FIGURE TEN: Particulate feeding by *Engraulis capensis* upon mixed size assemblages of mesozooplankton.

(a) Exp. 3 *P. africana* 1.160mm (A) and C. carinatus (B) 2.285mm.

A) $y = 81.5 - 0.009t$ r=0.87
B) $y = 499.2 - 0.287t$ r=0.96

(b) Exp. 14 *A. salina* juveniles

	I	II
A) 0.740mm	$y = 403.8 - 0.015t$ r=0.92	$y = 4.108e5 - 0.092t$ r=1.00
B) 0.902mm	$y = 3351.0 - 0.022t$ r=1.00	$y = 2.687e8 - 0.148t$ r=1.00
C) 1.105mm	$y = 3013.9 - 0.041t$ r=0.98	$y = 5.769e6 - 0.130t$ r=1.00
D) 1.413mm	$y = 1068.5 - 0.264t$ r=0.87	

(c) Exp. 18 *A. salina* juveniles

	I	II
A) 0.725mm	$y = 813.2 - 0.018t$ r=0.98	$y = 3301.1 - 0.048t$ r=0.97
B) 0.893mm	$y = 1365.1 - 0.032t$ r=0.98	$y = 2.100e5 - 0.116t$ r=0.99
C) 1.071mm	$y = 1127.8 - 0.054t$ r=0.98	$y = 1.070e6 - 0.173t$ r=1.00
D) 1.261mm	$y = 231.4 - 0.320t$ r=0.95	

(d) Exp. 18 *A. salina* cysts 0.226mm (E) and *P. crassirostris* 0.484mm (F).

E) $y = 243.7 - 0.038t$ r=0.97
F) $y = 30.3 - 0.025t$ r=0.97

The clearance rate obtained for *P.hessi* (Exp. 6) may be an underestimate for particles of that size, because this copepod preferred to be situated near or on the walls or bottom of the tank during culture. This behaviour would make it less accessible to the fish during an experiment. The rates obtained for *A. salina* adults, on the other hand, may be overestimates, since *A. salina* does not possess the well developed escape response of similar sized zooplankters which make up part of the natural diet of *E. capensis*, such as the euphausiid *E.lucens*. *E. lucens* was not used an an experimental food, because the majority of the prey settled to the bottom immediately after introduction to the tank. This behaviour is typical of *E. lucens* maintained in the laboratory (Pillar pers. comm.).

When mixed size assemblages of food were offered to the fish, the clearance rates of the largest foods were high and similar to expected values, while those of the smaller particles were initially only ±30% of the expected values,but increased after the complete removal of the largest food available (Table 6; Fig. 10 Exp. 14 and 18). These results indicate that the fish direct their attention towards the largest available food, ignoring the smaller items and hence suppressing their clearance rates until the preferred food is removed. There was a lag period of 40 - 60 minutes between the erradication of the largest food available and the increase in the clearance rates of the smaller

particles (Fig. 10). This was presumably due to the fish continuing to search for its preferred prey, for which it had developed a search image, and to the fish readjusting their search mode for the smaller prey. There were no obvious changes in feeding behaviour during the experiments. After the removal of the largest prey, the clearance rates of the remaining food sizes were closer to expected values (Table 6). It will be noted that, in all but one instance (Exp. 14B and C), the clearance rates before and after the removal of the largest prey increased with increasing particle size.

The clearance rates of similar sized particles were markedly more variable during the biting trials than during the filtering ones (Table 6; Fig. 9 and 10). The clearance rates of *C. carinatus* and *A. salina* adults varied by 56% and 80% respectively in consecutive experiments (Table 6). Variations in swimming speed, prey size and concentration cannot be invoked to account for these differences, and, except for the light regime during Exp.10, the experimental conditions were identical in all respects. They are possibly due to unquantified differences in feeding behaviour caused by factors such as disturbance, state of hunger or feeding history. One interesting fact is that in both cases the clearance rates were higher during the second experiment. Both pairs of trials were run on consecutive days, with no feeding taking place in between. It is possible that a search image developed during the first experiment persisted and enhanced the rate of capture

during the following trial. Observations during the collection of the reactive distance data indicated that the fish formed a search image for a prey type that was offered several times in succession, but there are no data about the length of time an image persists.

Clearance Efficiencies

The clearance efficiency (Durbin and Durbin 1975) data are presented in Table 6. The method of assessing filtering efficiency for the present data differs from that employed by Durbin and Durbin (1975), who defined the maximum filtration rate (Fmax) as the total volume of water passing through the gill rakers, i.e. the product of the swimming speed and mouth area, stating that a particle being retained with 100% efficiency by the gill rakers would have this clearance rate (F = Fmax). The filtering efficiency of the gill rakers for any particle was then the ratio of F to Fmax. This probably overestimated Fmax as it assumed that the fine mesh of the gill raker mechanism - in the case of *B. tyrannus* with the majority of the pores less than 80 µm (Durbin and Durbin 1975) - offered no resistance to the flow of water through the mouth and opercula. This is not the case, even though the tulip - shape of the mouth observed by Gibson and Ezzi (1985) would partially compensate for the resistance generated by the filtering mechanism by acting as a mouth-reduction cone similar

to those used with high speed plankton samplers (Tranter and Smith 1968). Thus the flow rate through the filtering system will be lower than that through the hollow cylinder of identical dimensions assumed in their calculation of Fmax. Therefore, the filtering efficiencies calculated by Durbin and Durbin (1975) are underestimates. For the present data, it has been assumed that the particle producing the maximum clearance rate was retained with 100% efficiency and therefore this clearance rate approximates Fmax. The ratio of the F values of the other particles to this Fmax provide a measure of the filtering efficiency of the anchovy feeding on different particle sizes.

Two approaches were taken to calculate Fmax for particulate feeding (Table 6): In the first Fmax was considered to be a product of the visual field and swimming speed of the fish (Rosenthal and Hempel 1970; Ware 1978; Durbin 1979). Ware (1978) noted that many factors may influence the visual field of the predator, such as counter shading in the water column and colouration and size of the prey. Data collected during the present study (Fig. 4) indicate that the reactive distance (Holling 1966) which can be considered as the extent of the visual field to which prey will be perceived and acted upon, is related to prey size. Therefore, Fmax could be defined as the product of the "reactive field" (Holling 1966) - a circular area with a radius equal to the reactive distance for that prey size determined from the relationship illustrated in Fig. 4 - and the swimming speed

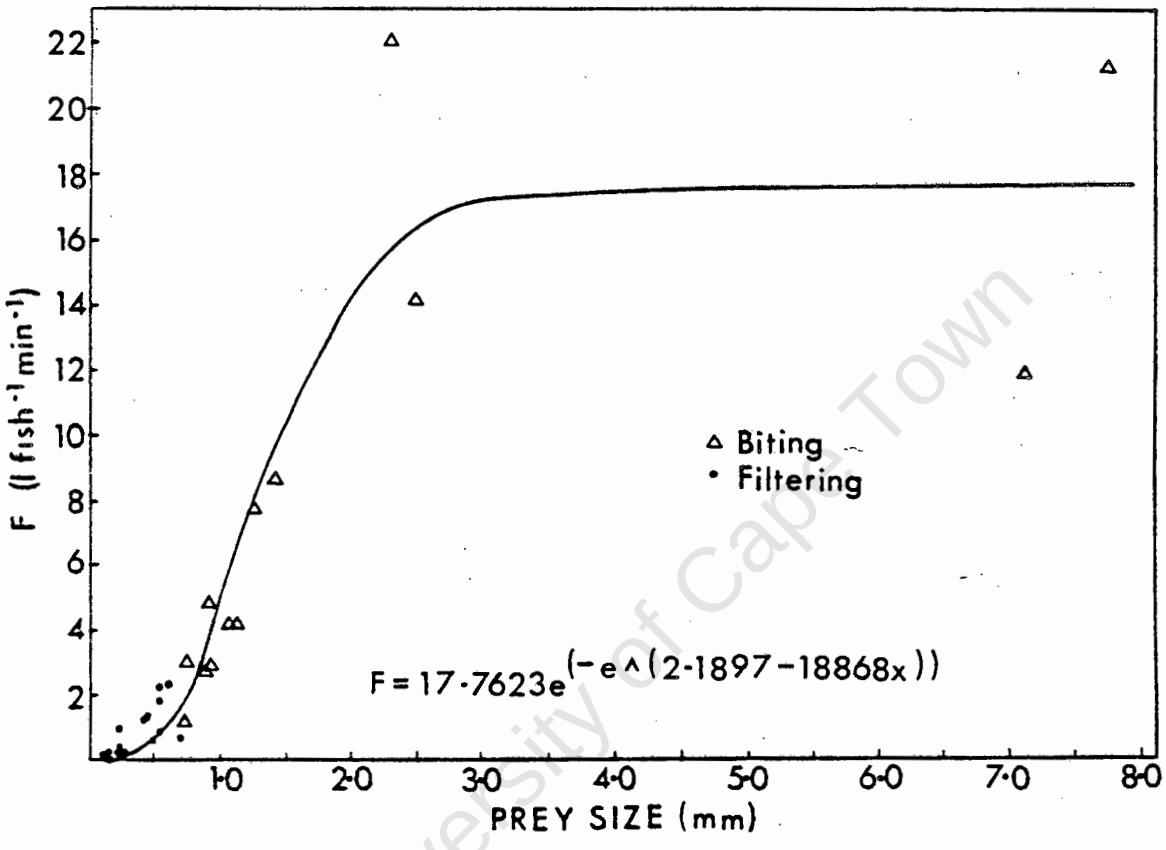


FIGURE ELEVEN : Clearance rates (F l/fish/min) of Cape anchovy as a function of prey size (mm).

(Table 2). In the second approach the asymptote of the Gompertz model of the observed F against particle size (Fig. 11) for all the experiments was assumed to be Fmax and all the observed F values were compared to this. It was considered appropriate to treat all the data *en masse* because of the similarities in their functional relationships (Figs. 6 - 10). This empirical approach does not provide an absolute estimate of feeding efficiency, since particulate feeding rates should be affected by prey concentration (E.G. Durbin pers. comm.). However, under the present experimental conditions, where prey concentrations were high and the fish effectively covered the entire tank during feeding, the observed maximum feeding rate probably appr- oximates Fmax. A measure of the efficiency of particulate feeding upon any prey would then be the ratio of the observed F to the calculated Fmax. This definition assumes that factors such as handling time, prey escape responses and competition between fish for the same prey item are negligible. Several experimental observations substantiate these assumptions:

1 all sizes of prey presented to the fish were ingested intact and there was no obvious handling or orientation of the prey in the mouth before swallowing. Field samples also indicated that prey were swallowed whole (Chapter two).

2 the maximum dimension of even the largest prey were considerably less than the height and breadth of a 100mm anchovy's mouth.

3 the swimming speed of the predator was at least 1 order of

magnitude greater than that of its prey. The swimming speed of the euphausiid, *Euphausia pacificus*, which is similar in size to *E.lucens*, ranges between 0.75cm/s and 3.11 cm/s (Torres and Childress 1983) compared to the cruising speed of 17cm/s ± 5.93 and the biting speed of 24.21 ± 7.02cm/s (Exp.18) of *E.capensis*.

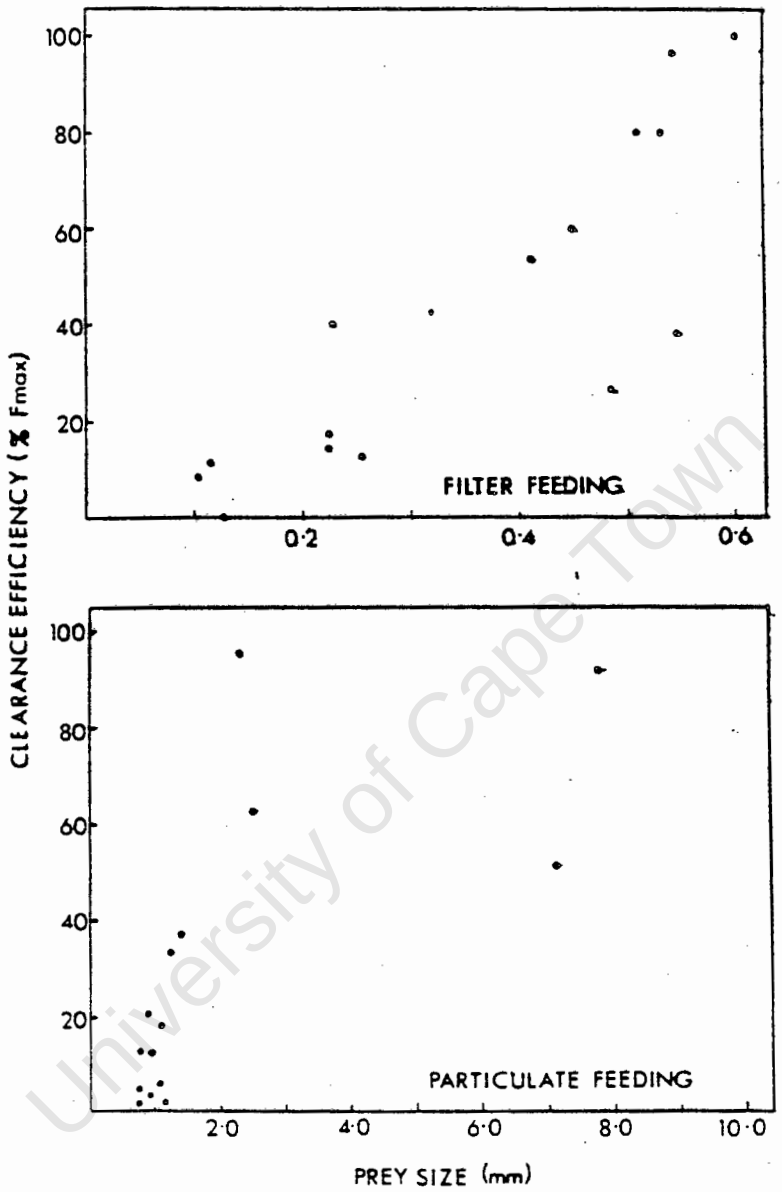
4 observations of particulate feeding fish indicated that biting attacks were rarely unsuccessful during the tank experiments and that two or more fish seldom, if ever, attempted to attack the same prey item.

5 both biting and filtering result in an exponetial decay in the concentration of food in the water. This similarity in the functional relationships indicate that handling and prey escape responses, which are non-existent during filtering are also unimportant during biting. Cushing (1978) and Pepin and Koslow (unpublished manuscript) have also suggested that handling time and prey escape responses are unimportant factors when considering planktivorous fish.

During experiments where mixed size assemblages of food were presented to the fish, it was assumed that the smaller particles were ingested while the fish searched for the largest prey available, and hence all the observed F values were compared to the Fmax value calculated for that particle.

The Fmax and clearance effeciency data are displayed in Table 6

FIGURE TWELVE : Clearance efficiencies for filter and particulate feeding by Cape anchovy during all feeding trials.



and Fig. 12. The filtering efficiency is largely dependent upon the geometry and range of sizes of the pores of the gill rakers relative to prey size (Durbin and Durbin 1975), and the results seem to reflect the increasing efficiency of retention of a filtering mechanism with a range of pore sizes (Fig. 12). However, the variability of the results demonstrate that filtering efficiency is not governed merely by pore and prey size, as intimated by Durbin and Durbin (1975), but that aspects of feeding behaviour such as swimming speed and the duration and frequency of filtering bouts, which vary both within and between trials, also have a major influence.

Of the two approaches used to estimate Fmax and clearance efficiencies of particulate feeding, only one produced meaningful results (Table 6 and Fig. 12). The method using reactive distances to estimate Fmax produced clearance efficiencies ranging from 2500 % to 0.3%; generally grossly over estimating the efficiency for small particles and underestimating it for larger ones. These efficiencies bore no resemblence to the observed clearance rates. A possible explanation for the failure of this method is that the high density of fish in the tank led to such large overlaps in the visual fields of the individual predators that the reactive distance model (Holling 1966) was not appropriate for analysing the data (E.G. Durbin pers. comm.). This situation occurs to some extent in the field, even when the fish are dispersed for feeding (Eggers 1976) and causes a reduction in the

rate of consumption of prey in schooling predators compared to individuals. The second method employing the asymptote of the F vs particle size plot (Fig. 11) as Fmax provided more realistic results (Table 6 and Fig. 12). During biting, the clearance efficiency increased rapidly with increasing particle size up to a maximum value at ±2.5mm. Again there is a great deal of variability in the data which is caused by differences in feeding behaviour such as preferential feeding upon the largest particle available, visibility of prey and rate of biting.

The attainment of a maximum feeding efficiency during biting suggests that factors such as the rates of striking, mouth opening and swallowing prey rather than location of prey may define the upper limit of the rate of particulate feeding in *E.capensis*, especially in the present experimental design, where light was not a limiting factor and the predators and prey were confined in a relatively small vessel.

DISCUSSION

The observations of feeding behaviour described here for *E.capensis* are similar in many respects to those recorded for other intermediate microphagists such as *E.mordax* (Leong and O'Connell 1969; O'Connell 1972; Hunter and Dorr 1982), *Scomber japonicus* (O'Connell and Zweifel 1972), *B. tyrannus* (Durbin and Durbin 1975), *Alosa pseudoharengus* (Janssen 1976; 1978), *Dorosoma petenense* (Holanov

and Tash 1978) and *C.harengus* (Gibson and Ezzi 1985). The major difference being that *E. capensis* was not observed to filter feed on large particles when present in high densities and switch to biting when this density was reduced below a threshold concentration as described for other planktivores (O'Connell 1972; O'Connell and Zweifel 1972; Hunter and Dorr 1982; Gibson and Ezzi 1985). During only one experiment were the two feeding modes observed simultaneously (Exp.16) when the fish commenced filter feeding and later in the experiment when food densities were reduced, alternated between filtering and biting. Possibly the switch from filtering to biting with decreasing prey density only occurs in *E.capensis* over a very limited size range of prey approximating the threshold size of 0.710 - 0.720 mm associated with the observed switch in feeding behaviour from filtering to biting, within which the energy gain versus the expenditure to acquire a particle at any concentration dictates the feeding mode employed. Gibson and Ezzi's (1985) conclusion that *C.harengus* switched from filter feeding to biting when prey density was reduced below a threshold level were based on experiments using one prey size and type (*A. salina* nauplii). The results of the present study, using a wide range of prey sizes and densities, indicate that their work might not be representative of the feeding repertoire of *C.harengus*, but described a special case where the prey used fell within a narrow band of prey sizes where density and size interact to determine the feeding behaviour displayed by the fish. O'Connell (1972) stated that when *E. mordax* was presented with a mixture of

A.salina nauplii and adults, biting replaced filtering behaviour, with filter feeding only increasing in intensity after the removal of the adults. This observation is in agreement with the findings of the present study, during which no active filter feeding occurred when the fish were presented with a wide range of food sizes (Exp. 18).

The loose aggregations observed during biting activity have been noted for other planktivores. Hobson (1968) stated that the flat iron herring, *Harengula thrissina*, fed on midwater crustaceans while in scattered layers. Longhurst (1971) and O'Connell (1972) noted that *E. mordax* schools were more diffuse when the fish were feeding on large particles and O'Connell (1972) and Eggers (1976) stated that this increased the fishes' encounter rate with their crustacean prey. This behaviour is also advantageous as it decreases the overlap of the visual fields of the fish (Eggers 1976; E.G. Durbin pers. comm.) and allows all the fish to feed effectively upon the available prey - if the fish remained in a tight school the potential volume searched would be considerably reduced and the fish at the leading edge would remove the bulk of the food, there by reducing the following fishes' consumption rate.

The observations concerning bottom and surface feeding by *E. capensis* provide the first descriptions of these types of feeding behaviour by anchovy. Several field studies have found evidence of these feeding modes in engraulids: Bayliff (1963) found quant-

ities of mud and benthic diatoms in the stomachs of *Cetengraulis mysticetus* from the Gulf of Panama; de Ciechomski (1967a; 1967b) stated that *Engraulis anchoita* displayed iliophagus feeding tendencies and James (Chapter two) found the benthic diatom *Triceratium favus*, fine mud and a dipteran wing in the guts of *E. capensis* from St. Helena Bay - evidence of both iliophagy and surface feeding.

The levels of food required to initiate filter feeding in *E.capensis* were lower than those required by *B. tyrannus* (Durbin and Durbin 1975), but greater than those for *E. mordax* (Hunter and Dorr 1982). These data suggest that there may be a progression in adaptation to unstable environments with patchy food environments from *B. tyrannus*, which inhabits eutrophic coastal environments, through *E. capensis* to *E. mordax* which occupy pulse and belt upwelling systems. One would expect the positions of *E. capensis* and *E. mordax* to be reversed. The Southern Benguela pulse upwelling system is less stable than the Southern Californian system, which is "downstream" of the Central Californian and Oregon upwelling areas and as such benefits from their "exported production" as well as that from temperate offshore waters advected southwards by the California Current (Shelton 1985). The disparity is probably due to the different criteria used to stipulate the threshold concentrations during the two studies. During the present study at least 50% of the school had to be observed to be feeding, while Hunter and Dorr (1982) only sought a significant

TABLE 7: The biomass of potentially available food for *Engraulis capensis* in the Southern Benguela Region. Data derived from recent plankton surveys. The 0 - 0.2mm and 0.2 - 0.5mm size categories contain the bulk of the phytoplankton and microzooplankton biomasses respectively.

SAMPLE AREA	STATION	BIOMASS µg DRY WEIGHT/L										
		Diatoms	Total Phyto	Copes. >0.30mm	Euph.	0-0.2	0.2-0.5	0.5-2.0	0.5-1.6	2.0-5.0	1.6-3.5	5.0-10.0	3.5+	10-15	15-20 mm
N.Benguela (Zernova 1974, from Shannon and Pillar 1986)			600-1560												
Cape Peninsula (Andrews and Hutchings 1980)			672.7												
(Shannon and Field 1884)			540-600												
U.M. Line (Mitchell-Innes *et al* in prep)	2	15.0	712.6												
	6	7.5	285.0												
	8	450.5	750.1												
St.Helena Bay/ C. Columbine				11.7	11.6										
				*261.4	233.0										
Cape Peninsula				8.7	4.6										
				*303.4	52.8										
Agulhas Bank (Pillar 1986)				6.1	2.7										
				*55.8	35.0										
West coast (Verheye and Hutchings 1988)							4.57		11.7		3.51		16.38		
South coast (Verheye in prep.)							2.92		10.27		1.62		1.01		
St.Helena Bay April 1984 (Chapter two)	03-24					194.0	168.4	185.4		39.71		0.32		2.13	-
	06-12					232.2	123.6	2.34		1.29		0.01		0.01	-
	08-06					162.5	87.89	28.29		2.94		0.77		4.36	-
	08-12					394.5	210.4	9.66		0.05		0.11		0.23	-
	08-18					658.7	66.32	86.84		8.37		25.6		10.44	-
	08-24					546.0	238.3	292.41		23.08		14.51		0.98	-
May 1984	01-24					425.9	23.12	22.68		9.38		70.28		75.26	-
	02-06					191.1	49.57	434.28		0.95		7.51		31.04	1.05
	02-12					87.5	28.18	0.98		0.13		0.01		0.76	-
	02-18					89.38	19.53	220.25		64.81		9.8		59.7	31.8
	02-24					111.7	23.02	129.92		0.72		40.35		271.75	86.32

* Maximum biomass values recorded by Pillar 1986.

difference between the initial and final concentrations of food in the tank over a 9 or 18 minute period, although the incidence of filtering could be very low. In only one instance was the incidence of filtering above 50% during the *A. salina* trials and in all the *Gymnodinium* trials the incidence of filtering was less than 10% and may have just been gaping activity. The threshold concentrations determined by Hunter and Dorr (1982) would be considerably higher if a 50% incidence of filtering was stipulated. The thresholds determined by Hunter and Dorr (1982) for anchovy eggs, on the other hand, are spuriously high since the anchovy will particulate feed upon eggs at much lower densities.

The food densities required to initiate filter feeding by *E.capensis* were generally exceeded in the field during recent plankton surveys (Table 7). Experimentally derived thresholds were between 5.1 µg dry wt./l and 67.85 µg dry wt./l (Table 4), while field values ranged from 87.5 µg dry wt./l (station 02-12, May 1984: Chapter two) to 1560 µg dry wt./l (Northern Benguela; Zernova 1974 [in Shannon and Pillar 1986]). This fact is, however of debatable ecological significance since the presence of larger particles which stimulate biting activity will have the dual effect of:

A. suppressing directed filter feeding activity upon the smaller particles, but

B. increasing the "incidental" consumption of these particles as

the fish pursue the larger prey. The data from the present study indicate that the accidental clearance rates of the microzooplankton and phytoplankton are greater than the directed rates (c.f. A.salina cyst clearance rates from Exps. 15, 16 and 18). Field evidence for the accidental consumption of phytoplankton and microzooplankton has been presented for *E.capensis* (Chapter two) and other planktivores (Parr 1930; Cushing 1978).

The replacement of filtering by biting when mixed size assemblages of food are available suggests that filtering may only be of importance when either there are no large particles present in the water or when feeding activity is low. James (Chapter two) noted that filtering activity in *E.capensis* was highest when overall trophic activity was low. O'Connell (1972) and Angelescu (1982) made similar observations for *E. mordax* and *E. anchoita* respectively. However the acquisition of food by filtering must not be underestimated. The present experimental and field data (Chapter two) demonstrate that the incidental intake of small particles during particulate feeding can be substantial.

The termination threshold levels found during this study may similarly be of limited value and little more than artefacts of experimental design since in the field the fish will continue to consume small prey below the laboratory determined threshold levels as long as there are large particles (>0.720mm) present

which stimulate particulate feeding.

The clearance rate data are adequately described by a Gompertz model (Fig. 11), with no discontinuity between the filtering and biting rates. The disparity between the minimum size for microzooplankton (0.129 - 0.256mm) and phytoplankton (0.093 - 0.1026mm) that could be effectively filtered from the water is of interest. *Chaetoceros* sp possess strong elongate setae which increase the size of the cell considerably, depending upon the species (Cupp 1943). The similarity between the clearance rate of the 10 cell chains of the *Chaetoceros* sp (0.114mm) monoculture and that of *B. plicatilis* (0.256mm) suggest that the setae doubled the dimensions of the algal chains. Therefore the minimum size that the anchovy can filter is approximately 0.200 - 0.250mm maximum dimension rather that 0.100mm. This coarseness of the anchovy's filtering mechanism precludes it from consuming a large proportion of the phytoplankton standing stock in the Southern Benguela (Table 7). Only large dinoflagellates and diatom cells and chains, or species with long setae will be available to *E. capensis*, and even these can only be filtered with very low efficiencies (Table 6). The smaller flagellate and diatom populations will be untouched by the anchovy. These findings could imply a resource partitioning between the anchovy and its major food source - herbivorous and omnivorous zooplankton (Chapter two). However, King and Macleod (1976) and James (Chapter two) found many food items less than 0.200mm in the stomachs of

TABLE 8: Filtering clearance rates of *Engraulis mordax, Brevoortia tyrannus* and *Clupea harengus*.

SPECIES	SAMPLING METHOD	PREY TYPE	PREY SIZE mm	PREY CONCS. INITIAL µg DRY WEIGHT/L	PREY CONCS. TERMINAL µg DRY WEIGHT/L	CLEARANCE RATE L/FISH/MIN	SOURCE
E. mordax	Gut analysis	*A. salina*	0.400	-	-	1.86+ 1.46#	Leong and O'Connell 1969 (+ own calculation, # O;connell 1972)
	Reduction sampling	*E. mordax* eggs	1.340	30-60	-		Hunter and Dorr 1982
		A. salina	0.433	8.5-3.1	-		
		Gymnodinium	0.040	1.8-3.8	-		
B. tyrannus *	"	*Dunaliella tertiolecta*	0.0091	-	-	-	Durbin and Durbin 1975
		Carteria chuii	0.0132	-	-	-	
		Skeletonema costatum	0.0078	-	-	-	
			0.0165	-	-	0.04	
			0.0291	-	-	0.10	
			0.0370	-	-	0.19	
			0.0491	-	-	0.18	
			0.0556	-	-	0.36	
		Thalassiosira rotula	0.0190	± 2520	± 1980	0.10	
			0.0442			0.18	
			0.0703			0.40	
			4 cell chain			0.36	
		Ditylum brightwelli	0.079	± 225-234	± 90-107	0.69	
		A. salina	0.430	-	-	1.28	
						1.35	
		A. tonsa	1.200	± 68		2.94	
						2.99	
						3.88	
						4.68	
C. harengus	"	*A. salina*	± 0.4-0.5	± 82		0.3-1.3	Gibson and Ezzi 1985
						0.72 ± 0.38	

* Filter feeding rates adjusted to account for differences in mouth area and swimming speed between *B. tyrannus* and *E. capensis* as follows:

$$\text{Adjusted clearance rate} = F^* \times \frac{Am}{Mm} \times \frac{As}{Ms}$$

Where F* is the measured clearance rate of *B. tyrannus* (Durbin and Durbin 1975)
Am is the mean mouth area of 10.04 cm anchovy (2.84 cm²)
Mm " " " " " " 25.70 cm menhaden (8.93 cm², Durbin and Durbin 1975)
As " " " swimming speed of feeding anchovy: phytoplankton - 16.39 cm/s (Exp. 19);
A. salina - 19.27 cm/s (Exps. 4 and 8);
copepods - 29.44 cm/s (Exp 3a).
Ms is the mean swimming speed of feeding menhaden: phytoplankton 42.92 cm/s;
A. salina 51.4 cm/s;
A. tonsa 64.25 cm/s (Durbin and Durbin 1975)

E. capensis from the south and west coasts of South Africa. The pore sizes of the gill rakers may vary with the degree of mouth opening; becoming smaller as the mouth closes after a biting attack and pushes the water through the filtering mechanism, thus trapping smaller particles. The coarseness of the gill rakers observed during directed filtering suggest that this feeding mode may only be used in the wild to prey upon aggregations of micro-zooplankton.

The filtering clearance rates of *E. capensis* obtained for *A. salina* are similar to those of *E.mordax* (Leong and O'Connell 1969) and to the rates of *B. tyrannus* (corrected for the differences in swimming speed and mouth area between the 2 species, Durbin and Durbin 1975) and are greater than those of *C. harengus* (Gibson and Ezzi 1985, Table 8). The clearance rates of small particles are greater for *B. tyrannus*, while that for the larger *Acartia tonsa* is less than the rate of an equivalent sized particle consumed by *E. capensis*, illustrating both the finer filtering mechanism of the menhaden and the switch from filtering to biting by the anchovy respectively. There is no leveling off of the filtering rate of the anchovy with increasing particle size as found for the menhaden (Durbin and Durbin 1975) - the anchovy's filtering rates continue increasing until the feeding behaviour switches to biting.

The data indicate that clearance rates increase rapidly between

the threshold size of 0.200mm - 0.250mm and an upper threshold of 2.500mm, after which it attains a maximum (Fig.11). James (Chapter two) found that the bulk of the anchovy's diet was between 1.0 and 15.0mm, indicating that the anchovy generally particulate feeds at high or maximial efficiency. The fact that, although *E. capensis* is primarily a visual predator, light intensity appeared to have no effect on the biting clearance rates agrees with the findings of James (Chapter two) who observed that the peak feeding times of *E. capensis* were between dusk and midnight on the west and midnight to midmorning on the south coasts. O'Connell (1963) demonstrated that the eye of *E. mordax* was well adapted to dim light vision and Hunter and Nicholl (1984) calculated that there was enough light at 30m depth in chlorophyll poor water (0.24mg Chla/ m^3) on a starlit night to allow the visual cues required for schooling and spawning in *E. mordax* to operate. Hunter (1968) stated that *Trachurus symmetricus* obtained 50% of its ration during low light conditions similar to that of surface coastal waters at night under a full moon. It is also possible that another sensory organ, such as the lateral line, plays an important role in prey location in low light conditions. The indication that vision and prey location are not important to the anchovys' clearance rates are an artefact of the experimental conditions. In the field, where visibility is lower than during the feeding trials and the prey more heterogeneously distributed in relation to the fish, these factors will become important.

The data clearly illustrate the anchovys' ability to select food on the basis of size, as reported during recent field studies for *E. mordax* (Koslow 1981) and *E. capensis* (Chapter two). This selective feeding upon larger prey items through the suppression of the clearance rates of smaller particle sizes and the fact that the clearance rates are maximal over most of the range of prey sizes could have important ramifications in the field, as the predators' impact would be to select for plankton communities composed of smaller species. Such an effect has been observed in both marine (Durbin and Durbin 1975; Koslow 1981 and Hunter and Dorr 1982) and freshwater (Warshaw 1972 and Drenner and Des Noyelles 1982) systems. However, the present data also indicate that the anchovy can readily redirect its feeding activity towards smaller items. This laboratory finding is similar to field observations of the selective feeding behaviour of *E.mordax* (Koslow 1981), where the northern anchovy was observed to remove 95-100% of the largest prey available over a 100 fold range in prey size. James (Chapter two) presented field data which indicated that consumption of smaller prey was suppressed when the fish preferentially fed upon larger particles, but that the rate of consumption of filterable items, which were considered as an incidental catch as the fish pursued the larger prey, increased. This flexible and highly opportunistic feeding behaviour is advantageous in an unstable environment such as the Southern Benguela since the anchovy can maximise their intake of the large particles, which tend to be heterogeneously distributed (Alldredge

TABLE 9: Estimated ingestion rates by 10.04cm *Engraulis capensis* using laboratory derived clearance rates and data from recent plankton surveys. The clearance rates were calculated for the mid point value of each size category and adjusted for suppression (* reduced by 70%) or enhancement (** increased by 300%) due to the pursuit of the largest particle available. No adjustments were made to size categories with the maximum clearance rate.

	COPEPODS	EUPHAUSIIDS	0.2-0.5	0.5-2.0	0.5-1.6	2.0-5.0	1.6-3.5	5.0-10	3.5+	10-15	15-20 mm	TOTAL INGESTION RATE µg/fish/min	TIME TO ATTAIN 10% BODY WT Hrs
MEAN SIZE	2.00	12.00	0.35	1.25	1.05	3.50	2.55	7.50		12.50	17.50		
F	14.47	17.76	0.176	7.632	5.182	17.549	16.517	17.762	17.549	17.762			
"F"	4.34*		0.528**	2.29*	1.555*	5.265*	4.955*						
PLANKTON DATA 1													
A	50.6	206.8										257.4	16.9
	(1134.5	4138.5)										(5273.0	0.8)
B	37.9	82.4										120.3	36.3
	(1316.8	937.8)										(2254.6	1.9)
C	26.5	48.0										74.5	58.5
	(242.2	621.7)										(863.9	5.0)
2			2.4		18.2		17.4		287.5			325.5	13.4
3			1.5		16.0		8.0		17.7			43.2	101.0
4 APRIL 1984													
03-24			88.9	424.6		209.1		5.7		37.8		766.1	5.7
08-18			35.0	198.9		44.1		454.7		185.4		918.1	4.8
08-24			125.8	669.6		121.5		257.7		17.4		1192.0	3.7
MAY 1984													
01-24			12.2	51.9		51.8		1248.3		1336.8		2701.0	1.6
02-18			10.3	504.4		341.2		174.1		1060.4	564.8	2655.2	1.6
02-24			12.2	297.5		3.8		716.7		4826.8	1533.2	7390.2	0.6

F - Uncorrected clearance rates
"F"- Corrected clearance rates

1 - Pillar 1986
A St. Helena Bay/ Cape Columbine
B Cape Peninsula
C Agulhas Bank
Values in parentheses represent the ingestion rates calculated from the maximum biomass estimates found by Pillar (1986).

2 - Verheye and Hutchings 1988
West coast
3 - Verheye in prep.
South coast
4 - Chapter two
Peak feeding stations in St. Helena Bay in April and May 1984

et al 1985; Nicol *et al* 1987), as encountered.

Ingestion rates estimated from recent biomass data (Table 9) demonstrate that the anchovy could fulfill its daily requirement (±10% body weight/day; Shannon and Field 1985) by particulate and the associated "incidental" filter feeding in the Southern Benguela. These data also illustrate the requirement for small scale intensive sampling strategies rather than large scale plankton surveys (Pillar 1986; Verheye and Hutchings 1988; Verheye in prep.) for the purpose of investigating the trophic ecology of planktivorous fishes as these data are integrated over large vertical and horizontal ranges. Verheye (in prep) and Verheye and Hutchings (1988) provided more suitable data by vertically stratifying their samples over several 10's of metres, but even this does not account for the scale of patchiness of plankton which the fish can perceive, react to and utilise. Only more coordinated sampling stratgies e.g., those of Koslow (1981) and James (Chapter two) can provide such information. However, it must also be realised that biomass and standing stock estimates from plankton surveys only represent the survivors of fish predation. The crucial point, both in terms of attainment of daily ration and the effect upon prey communities, is the proportion of the production that is removed by the fish.

If the peak biomass estimates of Pillar (1986), when it appears that aggregations of prey were sampled (Pillar pers. comm.), are

used to calculate ingestion rates, the values are similar to those estimated using the data of James (Chapter two; Table 9). It is interesting to note that the time required to consume 10% body weight is greater on the south than on the west coast. This provides a possible explanation for the extended feeding period in the former area observed by James (Chapter two).

O'Connell (1972) suggested that filtering provided a continuous intake of food for *E. mordax*, with biting supplying the remainder of the daily ration. However, it is energetically uneconomic to filter continuously because of the high energy output required to sustain this mode compared to normal swimming (James Chapter five). It is energetically more advantageous for the fish to employ biting, which is less expensive (Chapter five) and provides a higher return. However there are large biomasses of phytoplankton and microplankton available for consumption in the Southern Benguela. It would appear that *E. capensis* has taken account of these energetic and trophic considerations by refining its feeding behaviour to the extent that, although it particulate feeds mainly upon mesozooplankton, it can simultaneously collect phyto- and micro-zooplankton using its gill raker mechanism, thus minimising energy expenditure and maximising gain.

SUMMARY

1) The results of this laboratory work corroborate the findings

of an earlier field study investigating the trophic ecology of *E. capensis* (Chapter five).

2) The schooling behaviour displayed by *E. capensis* during feeding enhances its feeding rate.

3) *E.capensis* acquires the bulk of its food by size selective biting upon items > 0.720mm, selecting for the largest available particle. This selection is achieved through the suppression of the clearance rates of the smaller particles.

3) The anchovy feeds at its maximum rate over most of the range of its trophic size spectrum.

4) The feeding behaviour of *E. capensis* is very flexible, allowing the fish to rapidly switch from filtering to biting and to redirect its size selective feeding to smaller items after the removal of the largest available prey.

5) The anchovy has refined its feeding behaviour such that it can simultaneously take advantage of the mesozooplankton, towards which it directs most of its feeding activity, and the available phyto- and micro-zooplankton.

CHAPTER FIVE

The relationship between respiration rate, swimming speed and feeding behaviour in the Cape anchovy, *Engraulis capensis*.

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TABLE 1: Summary of information concerning the conditions during the experimental trials.

EXP No	No FISH	MEAN LENGTH mm	TOTAL DRY WT g	TOTAL WET WT g	TIME STARVATION Hrs	FEEDING Hrs	FOOD TYPE	FOOD SIZE mm	RATION SIZE % BODY WEIGHT	RATE OF SUPPLY % / Hr
3	48	90.82	89.66	300.65	24	2.0	*Artemia salina* *Brachionus plicatilis* *Paracalanus crassirostris*	0.567 0.256 0.650	6.67	3.34
4	63	90.82	117.68	394.60	36	3.0	*B. plicatilis* *P. crassirostris*	0.256 0.339	1.25	0.42
8	26	100.40	70.20	243.62	48	2.5	*Paracalanus* sp.	0.750	1.30	0.52
9	28	100.40	75.60	262.36	36	3.0	*A. salina*	2.460	2.05	0.68
12	114	88.43	226.60	634.35	36	2.5	*A. salina* *Calanus finmarchicus*	2.100 2.147	1.87	0.75
14	101	88.43	202.54	634.35	36	3.0	Cladoceran	2.480	2.35	0.78
15*	101	88.43	202.54	634.35	24					
16*	113	88.43	224.62	628.79	24					
17*	113	88.43	224.62	628.79	24					
18*	113	88.43	224.62	628.79	24					

* Experiments conducted to determine a Respiratory Quotient (RQ) for *Engraulis capensis*.

INTRODUCTION

The Cape anchovy, *Engraulis capensis* comprises the bulk of the South African and Namibian purse seine fisheries. Earlier work has demonstrated that although *E. capensis* is generally a size selective, particulate feeding carnivore (Chapter two), it is capable of preying upon a wide spectrum of particle sizes by employing its gill raker mechanism either in conjunction with particulate feeding or by switching to the filterfeeding mode (Chapter four). Although this flexible feeding behaviour allows the anchovy to take maximum advantage of the available food, little is known about the relative costs of particulate and filter feeding.

A suite of experiments were conducted to measure the voluntary swimming speeds and respiration rates of *E. capensis* during four different states: routine activity, filterfeeding, particulate feeding and postfeeding activity. These experiments were part of a larger study to develop carbon and nitrogen budgets for the anchovy.

MATERIALS AND METHODS

Three batches of anchovy were captured and maintained in the laboratory as described by James (Chapter three; Table 1). The

experimental trials were conducted in a 2m diameter, 1.5m deep fibreglass tank covered by 55% shadecloth and subject to the ambient light cycle. The tank was supplied with a continuous flow of 5 µm filtered seawater at ambient temperature (16.2 ±0.4 °C).

Each batch of fish was maintained in the laboratory for three to six weeks before being used in the experiments. The fish were fed a daily ration of 6% - 7% dry body weight composed of dry trout pellets, a beef liver, anchovy or rock lobster offal mixture (Chapter four) frozen zooplankton and occasionally live *Artemia salina* and wild zooplankton when available. All the zooplankters used as experimental prey (Table 1) were raised in 200 - 2500l batch cultures.

Two different sets of experiments were conducted:

A) The first (Experiments 3, 4, 8, 9, 12, 14) investigated the relationships between respiration rate and swimming speed before, during and after feeding activity;

B) the second set (Experiments 15, 16, 17, 18) were carried out to provide data for the calculation of a respiratory quotient during routine activity; a value required to convert oxygen consumed to carbon respired for future carbon budget work.

The fish were starved for 24 - 48 hours before an experiment to permit the evacuation of the intestine and to ensure that the

last meal had no effect upon the metabolism of the fish during the forthcoming trial. The sides and bottom of the tank were thoroughly scrubbed and vacuumed the day beforehand to remove any attached growth. This procedure was repeated 2 - 3 hours before the start of the experiment, the tank flushed with filtered seawater and the water level adjusted to the required depth. Two 0.6m x 1.0m Lexan sheets graduated in 0.1m grids were placed on the tank bottom and a 3mm thick transparent Lexan lid, which fitted snugly with the sides of the tank, was gently lowered onto the water's surface, forming a simple closed system respirometer. The fish invariably reacted to the fitting of the airtight lid in a manner similar to the escape response described by Wilson *et al* (1987) for this species. Therefore the fish were allowed to settle for up to 2.5 hours after the fitting before initiating an experiment and the lid was removed or reset only when absolutely necessary. Refitting was followed by a period of "abnormal" activity, the length of which depended upon the state of preoccupation of the fish; if the lid was refitted when the fish were feeding the reaction period was short relative to the period ensuing a refitting during routine activity.

Each feeding experiment began with either simultaneous measurements of routine respiration rate and swimming speed (Exps. 3, 8, 9) or with a single measurement of swimming speed (Exps. 4, 12, 14). The fish were observed closely during this initial period to ascertain whether they had returned to routine activity levels after the

fitting of the lid. Food was then introduced to the tank and regular measurements of dissolved oxygen and swimming speed were taken during and for 20 - 24 hours after the feeding period.

The batch cultures of experimental food were concentrated into a 10l volume by gentle back filtration for input into the tank. Sub-samples of food were taken for determination of number of particles per litre, dry weight per litre, carbon and nitrogen and, when possible, calorific content (Table 1). The rate of supply of food to the tank was regulated such that the fish fed at an approximately constant rate for 2 - 3 hours, which corresponds to the peak feeding period in St. Helena Bay deduced by James (Chapter two). The food was delivered to the tank by displacing the fluid in the food vessel with air using an aquarium pump. The rate of supply of air to the food vessel, and hence the rate of flow of food to the experimental tank, was controlled by a needle valve. The food was continuously mixed to ensure a constant supply of food to the tank throughout the feeding period.

Three 125 ml water samples were taken at each time interval from 3 different points in the tank and 3 - 5 20ml subsamples from each were used to determine the dissolved oxygen content of the tank water using a modified Winkler technique (Parsons *et al* 1984). Half strength sodium thiosulphate solution (0.005 N) was used to increase the titre volume. The precision of the method was ± 0.016 $mgO_2 . l^{-1}$. Simultaneous oxygen measurments taken from

differing points around the tank indicated that it was well mixed by the swimming activity of the fish. A preliminary experiment with the tank containing filtered seawater and zooplankton demonstrated that the prey did not significantly alter the oxygen levels in the system during the feeding period.

Total carbon dioxide was determined using the method described by Parsons *et al* (1984). Three 125ml samples were taken at each time interval for CO_2 analysis. The precision of the method is given by Parsons *et al* (1984) as ± 0.012 milliequivalents l^{-1}.

Observations of swimming speed and schooling behaviour were made throughout the experiments. Swimming speeds were measured using an 8mm movie camera at 18 frames s^{-1} and the fish were photographed 1 - 3 times during each time interval for 10 - 15 second periods against the background of the 0.1m grids described above. Each 10 - 15 second sequence constituted a swimming speed measurement. The film was analysed using a microfiche reader at 34x magnification. A clear acetate sheet was placed over the microfiche screen and the progress of individual fish across a grid was plotted at 6 frame (0.33 s) intervals. A total of 600 - 1350 observations of swimming speed were made during each measurement. All observations within a measurement were tested for normality using the Kolmogorov - Smirnov D statistic and were pooled to provide a mean swimming speed ± 95% confidence limits.

TABLE 2: Oxygen consumption, carbon dioxide production and calculated RQ values from the four trials using unfed *E. capensis*.

EXP No	AMBIENT O_2 mg l^{-1}	% SATURATION OF TANK WATER	O_2 CONSUMED ml/ g wet wt/ Hr	CO_2 PRODUCED ml/ g wet wt/ Hr	RESPIRATORY QUOTIENT
15	4.62	82.35	0.511	0.540	1.060
17	5.46	97.33	0.190	0.181	0.953
18	5.67	101.07	0.225	0.179	0.796
16	5.95	106.06	0.146	0.124	0.849
MEAN					0.915 ± 0.183

The mean swimming speeds were plotted against the respiration rate to determine the relationship between oxygen consumption and swimming speed during the various states of activity. General linear models and functional (GM) regressions were fitted to the data. The slopes and elevations of the the regressions were tested for significance by analysis of covariance (Zar 1984). All statistics were executed using the Statistical Analysis Systems (SAS) Basics statistical package.

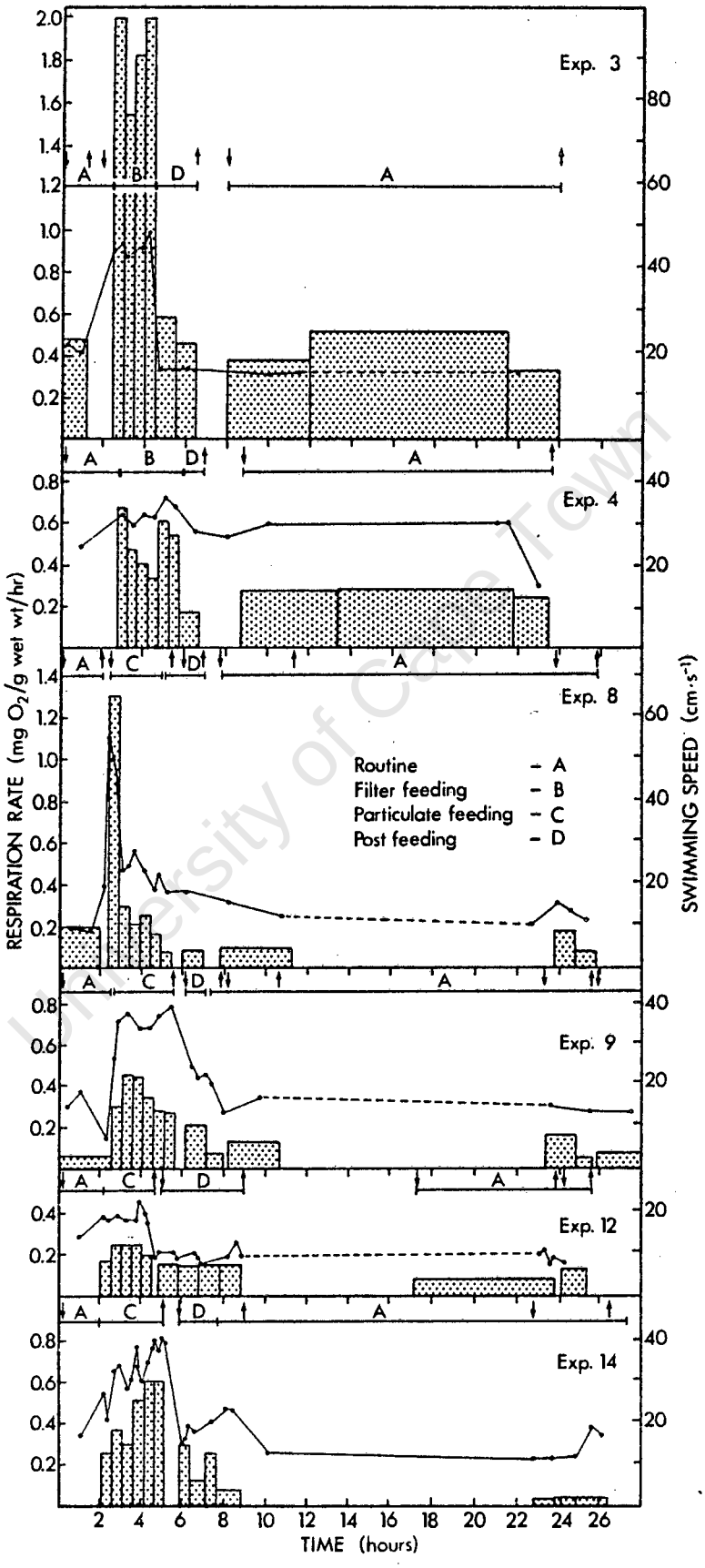
RESULTS

The results of the 4 RQ trials are displayed in Table 2. The mean value of 0.915 ± 0.183 suggests that protein was utilised as a metabolic fuel (Brett and Groves 1978).

The anchovy were fed rations ranging from 1.25% - 6.67% dry body weight during the 2 - 3 hour feeding periods corresponding to approximate rates of intake of 0.42% - 3.34% dry body weight per hour (Table 1). All the fish in a school behaved in a similar manner throughout a feeding experiment. Therefore we assumed that each fish obtained an equal portion of the available food.

All the experiments followed the same pattern (Fig. 1); generally both the respiration rate and the swimming speed increased immediately after the introduction of food, remained elevated

FIGURE ONE : Swimming speeds (line) and respiration rates (bar) recorded during each of the feeding trials. The activity states are indicated and the heavy black line on the X axis demarcates the period during which food was supplied to the tank. Arrows indicate when the lid was fitted (v) or removed (^).



throughout the feeding period and returned to routine levels soon after the termination of feeding.

There were several deviations from this general pattern. Routine respiration and swimming speeds measured during Experiments 3 and 4 were markedly higher than those recorded during the other experiments (Fig. 1). These fish were the first wild anchovy to be captured and maintained in the laboratory (Chapter three) and were observed to be considerably more excitable than later batches. The elevated initial measurements during Experiments 3 and 8 were due to these trials being commenced before the fish had completely settled after fitting the airtight lid. The full 2 hour settling period had been allowed, but the fish continued to display signs of excitement. In later experiments it was found that the fish settled more rapidly when occupied by feeding.

The data available (Experiments 3, 4 and 12; Fig. 1) give no indication of a significant reduction in respiration rates during darkness as reported for the Atlantic menhaden by Hettler (1976) and Durbin *et al* (1981). However, the data are sparse and further work is required to address this aspect of the anchovy's activity cycle. Observations during the experiments showed that the fish were less easily agitated at night and seemed to swim more slowly, although it was not possible to accurately measure this. The mean routine respiration rate and swimming speed for

TABLE 3: Respiration in excess of routine during the feeding and postfeeding periods and the equivalent carbon losses in relation to the carbon gained from the available ration. All values have been standardised against the dry weight of the fish.

FEEDING MODE	EXP No	RATION SIZE		RESPIRATION IN EXCESS OF ROUTINE					
				FEEDING			POSTFEEDING		
		mg dry wt/ g	mgC/ g	mgO_2/ g	mgC/ g	% RATION	mgO_2/ g	mgC/ g	% RATION
FILTERFEEDING	3	66.69	28.35	11.79	4.05	14.30	2.72	0.93	3.30
"	4	12.46	4.33	3.97	1.36	31.50	0.21	0.07	1.70
PARTICULATE FEEDING	8	13.03	1.56	2.91 1.16*	1.00 0.40	63.90 25.60	-	-	-
"	9	20.54	3.88	2.51	0.86	22.20	0.35	0.12	3.10
"	12	18.97	8.17	0.75	0.26	3.20	0.40	0.14	1.70
"	14	23.50	11.32	2.66	0.91	8.10	0.48	0.16	1.50

* The respiration rate of 1.305 mgO2/ g wet wt/ Hr measured during the feeding frenzy has been omitted and the respiratory losses calculated using the value of 0.298 mg O2/ g wet wt/ Hr, which was the respiration rate recorded after the termination of the frenzy.

food was left. Feeding frenzies were only observed during Exps. 3 and 8, when the rates of supply of food were greatest, and were associated with high respiration rates and swimming speeds. During the rest of the experiments the feeding behaviour was of a more consistent nature. Although the swimming speeds increased considerably during particulate feeding experiments, it was generally accompanied by a smooth motion with gentle turns, rather than the rapid darting movements and frenetic turning associated with the frenzy (Chapter four).

The metabolic cost of feeding may account for a significant portion of the carbon in the ration, especially during filterfeeding and when the ration was small (Table 3). The feeding frenzy during Experiment 8 accounted for 63.9% of the available carbon, and of this, 38.3% was respired during the first half hour of feeding (Table 3). Experiments 4 and 9 provide a comparison of the relative costs of the two feeding modes demonstrating that in terms of gain versus expenditure, particulate feeding is considerably more profitable (Table 3).

The fish rapidly removed the remaining food at the end of the feeding interval and a period of "searching" followed, designated the postfeeding period. This can be considered a transitional phase of activity when the fish tended to be agitated and schooled differently compared to the feeding and routine states. This period varied from approximately 1 hour (Experiments 4 and 8) to 4 hours

FIGURE TWO A : The relationship between swimming speed and respiration rate during routine activity. The 95% confidence limits are shown. The data are from all trials.
B : The relation between the mean swimming speeds and the coefficient of variation of the swimming speeds of the anchovy during routine activity.

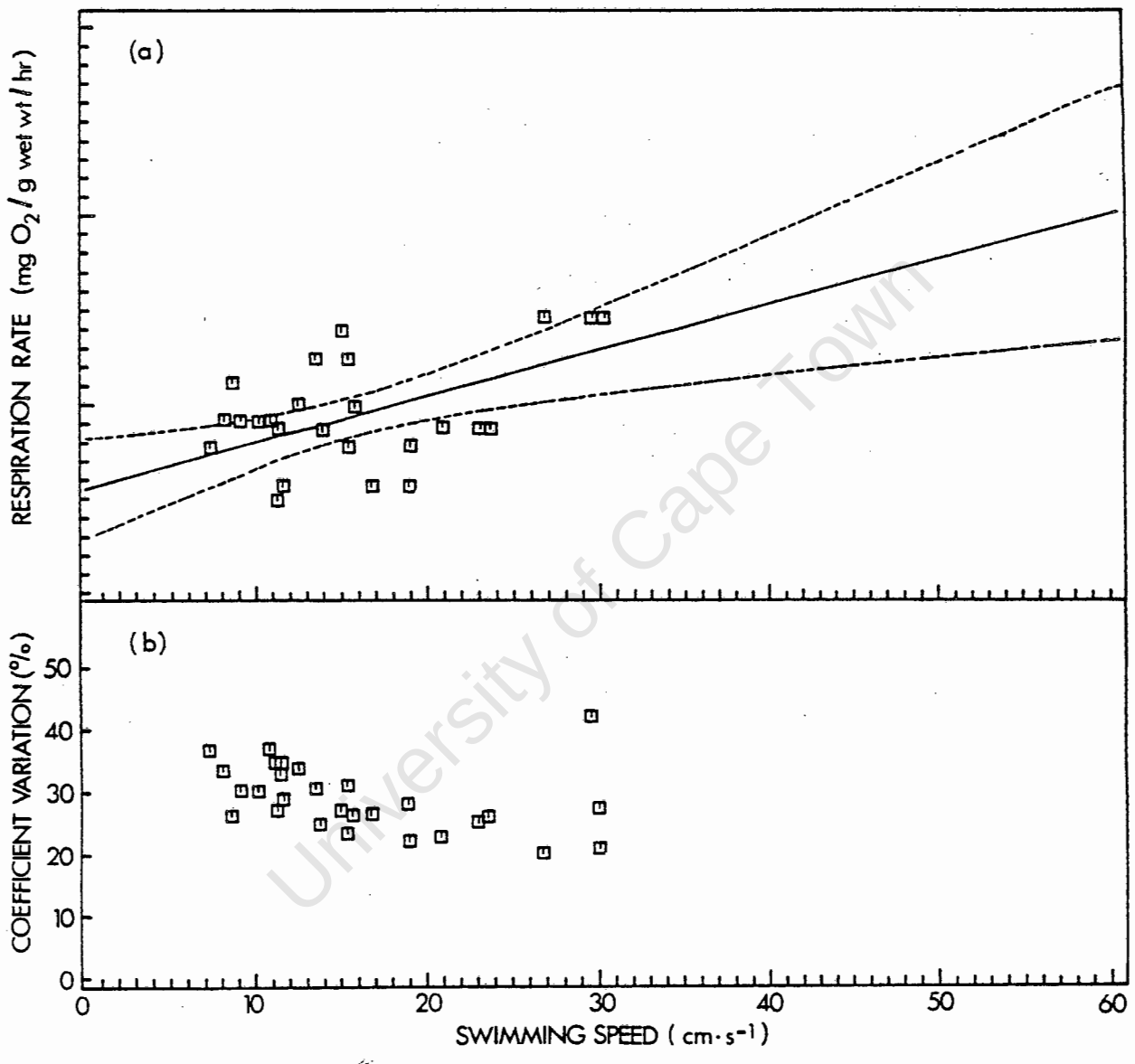


TABLE 4: The general linear models and functional (GM) regressions of the swimming speeds (S) and respiration rates (R) of *Engraulis capensis* during the four different activity states shown in Figs. 3 - 6. The mean values and 95% confidence limits are given for the routine and postfeeding periods.

ACTIVITY	GENERAL LINEAR MODEL	FUNCTIONAL (GM) REGRESSION	MEAN	
			S cm s^{-1}	R mgO_2/ g wet wt/ Hr
ROUTINE (Fig. 2)	log10 R = 0.024 S - 1.447 r = 0.542 S.E. slope = 0.0073		16.09 ± 2.67	0.111 ± 0.033
FILTERFEEDING (Fig. 4)	log10 R = 0.041 S - 1.618 r = 0.969 S.E. slope = 0.0033	log10 R = 0.042 S - 1.669		
PARTICULATE FEEDING (Fig. 4)	log10 R = 0.022 S - 1.138 r = 0.886 S.E. slope = 0.0019	log10 R = 0.025 S - 1.226		
POSTFEEDING (Fig. 5)	log10 R = 0.010 S - 0.909 r = 0.363 S.E. slope = 0.0057		15.62 ± 2.65	0.187 ± 0.0296

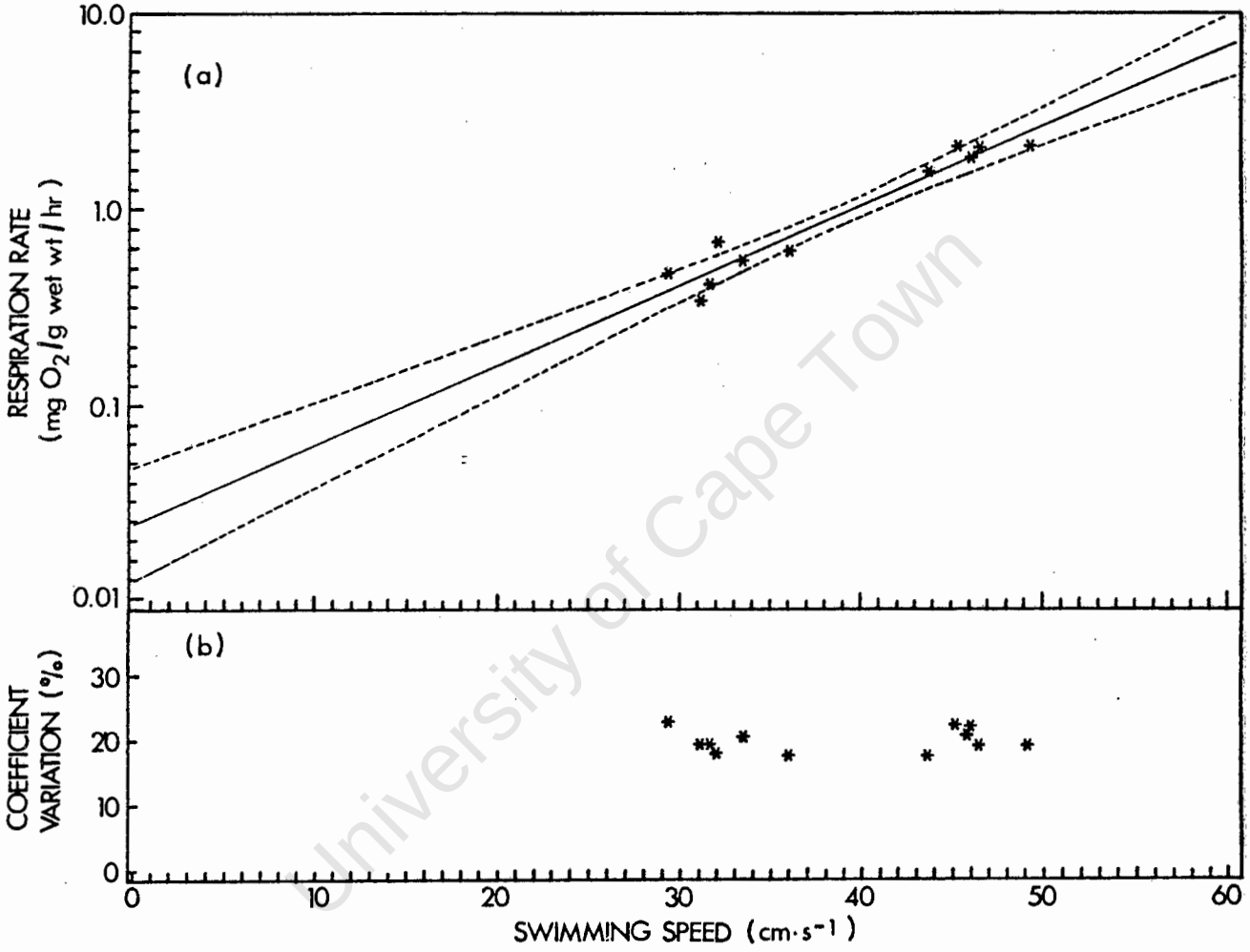
(Exp. 12; Fig. 1) and ended when the fish were observed to have returned to routine non - feeding behaviour (Chapter four). Postfeeding respiration rates and swimming speeds were erratic and could be greater or less than the routine values recorded during the same experiment (Fig. 1). Mean postfeeding measurements for all experiments were 0.187 ± 0.030 mgO_2. g wet wt^{-1}. hr^{-1} and 15.62 ± 2.65 cm s^{-1}, which were respectively slightly higher and lower than the routine values. Metabolic expenditure above routine during postfeeding was consistently low regardless of the duration of this period - accounting for 1.5% - 3.3% of the carbon available in the ration (Table 3).

Relationships Between Respiration Rate and Swimming Speed

Routine Activity.

There was a significant linear relationship between the routine respiration rates and swimming speeds ($r = 0.542$, $F = 10.83$, $P < 0.005$, Fig. 2A and Table 4). The plot of the coefficents of variation vs swimming speed showed that there was considerable variation about the means (Fig. 2B), suggesting many spontaneous changes in swimming activity. There was a tendency in the data for the smaller coefficients of variation to be associated with the faster swimming speeds (Fig. 2B).

FIGURE THREE A : The relationship between swimming speed and respiration rate during filterfeeding activity (Exps. 3 and 4). The 95% confidence limits are shown.
B : The relation between the mean swimming speeds and the coefficient of variation of the swimming speeds during filterfeeding.

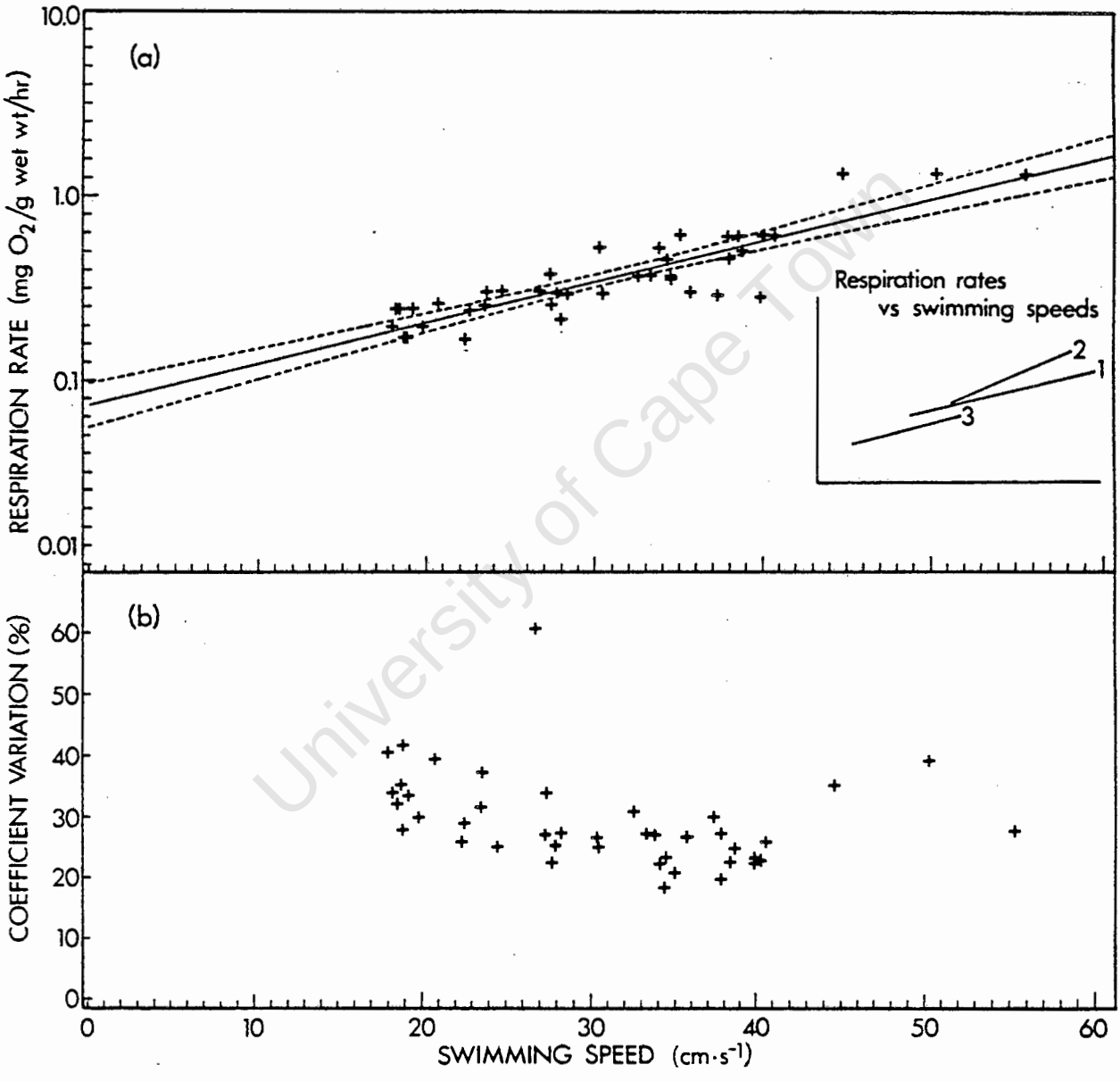


Filterfeeding

There was a good correlation between the filterfeeding respiration rates and swimming speeds ($r = 0.969$, $F = 152.22$, $P < 0.0001$ Fig. 3A and Table 4). Due to the bimodal distribution of the data (Fig. 3A) a Spearman rank correlation (Zar 1984) was calculated to test the significance of the fit ($rs = 0.941$, $P < 0.001$). Filterfeeding was the most consistent behaviour observed, shown by the coefficient of variation data which were the lowest recorded and remained constant over a wide range of swimming speeds (± 20% Fig. 3B). This is a similar result to that of Durbin *et al* (1981), who also found that the behaviour of the Atlantic menhaden was least variable during filterfeeding.

The slope of the relation between filterfeeding respiration rate and swimming speed was significantly steeper than both the routine and particulate feeding regressions ($t_{æ(2),36} = 5.849$ $P < 0.01$ and $t_{æ(2),50} = 18.269$ $P < 0.001$ respectively, inset Fig. 4), demonstrating that filterfeeding is bioenergetically more expensive than particulate feeding. This may be due to the change in body shape and the resulting drag when the mouth is held open with the opercula flared and water forced through the gillrakers during filtering.

FIGURE FOUR A : The relationship between the swimming speed and respiration rate during particulate feeding (Exps. 8, 9, 12 and 14). The 95% confidence limits are shown. Inset : A comparison of the swimming speed-respiration rate plots during 1) routine activity, 2) filterfeeding and 3) particulate feeding activity.
B : The relation between the mean swimming speeds and the coefficient of variation of the swimming speeds during particulate feeding.

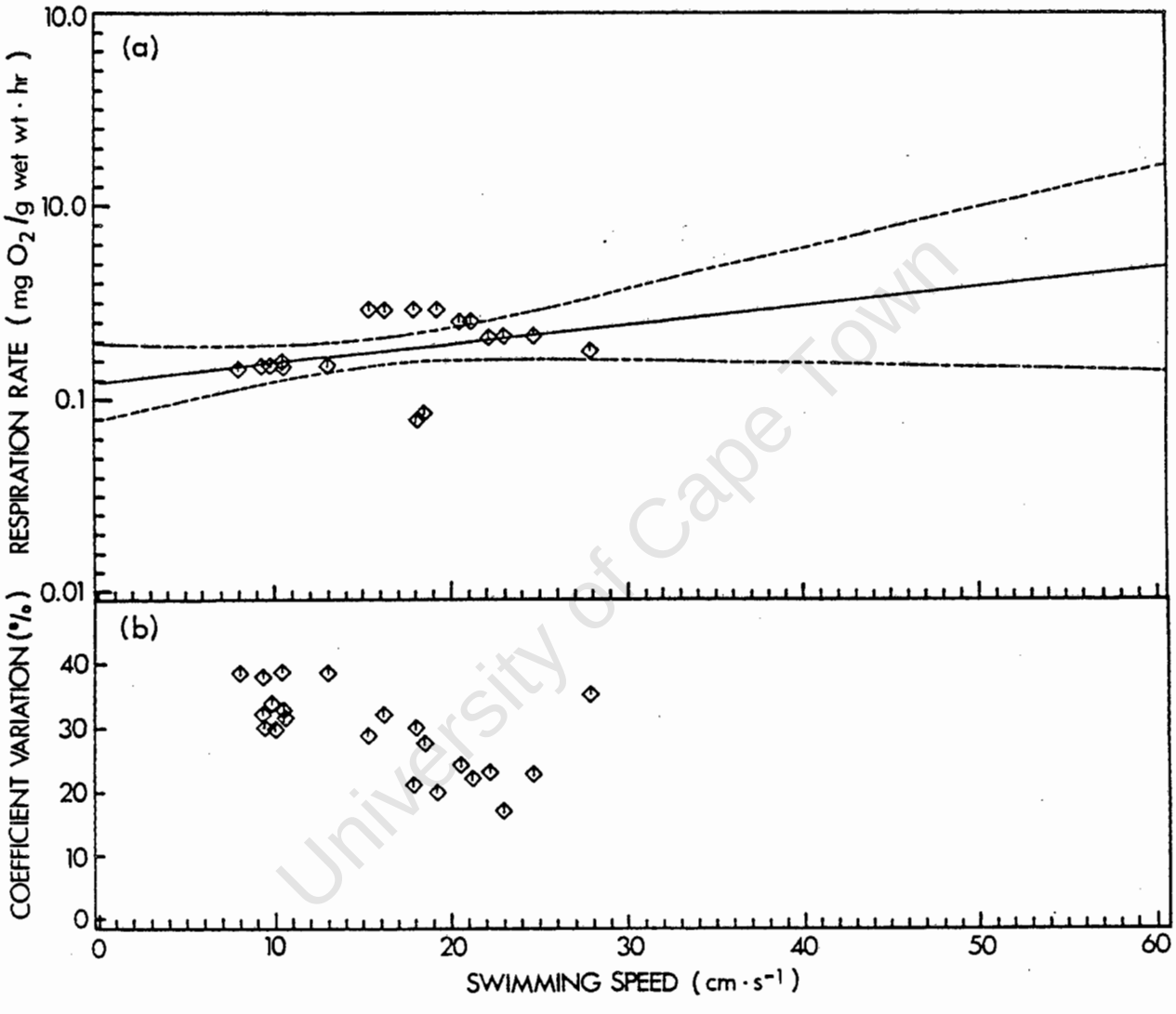


Particulate feeding

There was a significant linear fit between the oxygen consumption and swimming speed data collected during particulate feeding ($r = 0.886$, $F = 146.13$ $P < 0.0001$ Fig. 4A and Table 4). These data are more variable than the filterfeeding results due to the higher frequencies of fish turning and the subsequent changes in swimming speed during feeding associated with orientation towards and attack of prey items (Chapter four). This is borne out by the coefficient of variation vs swimming speed plot which displayed more scatter than the filtering data (Figs 3B and 4B). As with the routine data, there was a tendency for the faster swimming speeds to have lower coefficients of variation (Fig. 4B).

The slopes of the particulate feeding and routine respiration rates vs swimming speed plots were remarkably similar ($t_{æ(2),66} = 0.751$ $P > 0.05$, inset Fig. 4) but their elevations were significantly different ($t_{æ(2),67} = 2.305$ $P < 0.05$), indicating that there were similar increases in oxygen consumption per unit increase in swimming speed during both states of activity. This suggests that there was no increased drag or loss of streamlining associated with the rapid opening and closing of the mouth during biting. Particulate feeding and routine activity appear to be very similar energetically, or at least share many common factors that influence the metabolic costs of these states.

FIGURE FIVE A : The swimming speed-respiration rate relationship during postfeeding activity. The data are from all trials. The 95% confidence limits are indicated.
B : The relation between the mean swimming speeds and coefficient of variation of the swimming speeds during postfeeding.



Postfeeding

Postfeeding is a transitional phase between the feeding and routine activity states. There was a poor correlation between the postfeeding respiration rates and swimming speeds ($r = 0.363$, $F = 3.03$, $P > 0.05$, Fig 5A). The fish were most skittish and agitated immediately after the termination of feeding; this variability is to be expected during a transient and unpredictable phase of activity. As during routine and particulate feeding activity, there was a tendency for the faster swimming speeds to show less scatter about the mean (Fig. 5B).

DISCUSSION

This study clearly demonstrates that in *Engraulis capensis*, the particulate feeding mode is more efficient, in terms of energy gain versus expenditure, than filterfeeding. These data support the findings of James (Chapters one, two and four) and are in contrast to the earlier work of King and McCleod (1976) for this species.

The mean RQ value for the Cape anchovy of 0.915 ± 0.183 is similar to that reported for *Salmo gairdneri* at 15 °C (Kutty 1968), which is also an active swimming species.This result is also similar to that obtained by Durbin and Durbin (1981) for the Atlantic menhaden. The deduction that *E. capensis* uses protein as

a major source of metabolic fuel is consistent with other reports in the literature concerning the metabolism of teleosts (Kutty 1968, 1978; Watts and Watts 1974; Brett and Zala 1975; Durbin and Durbin 1981). Only Lasker (1970), quoting Hawke (1954), appears to differ, stating that the Pacific sardine, *Sardinops caerulea*, metabolises lipid. Durbin and Durbin (1981) estimated that 26.2% of the routine oxygen consumption of the Atlantic menhaden was used for protein catabolism. Kutty (1978) arrived at a similar conclusion for the sockeye salmon from the data of Brett and Zala (1975), estimating that protein oxidation accounted for 18% - 38% and 15% - 73% of the oxygen consumption in starved and feeding fish respectively. Kutty (1978) and Durbin and Durbin (1981) observed similar patterns in the O:N ratios during and after feeding and hypothesised that the fish studied obtained a large proportion of their energy requirements directly from the catabolism of amino acids absorbed during feeding.

The highest RQ value recorded of 1.06 falls outside the range of 0.7 - 1.0 cited by Brett and Groves (1978) for the aerobic utilisation of lipids, proteins and carbohydrates as metabolic fuels and suggests that the anchovy repired anaerobically during that trial (Table 2). However, it is unlikely that an active pelagic species would resort to such inefficient pathways to derive metabolic energy when the tank water was over 70% saturated with oxygen (Table 2). The accurate determination of changes in the concentration of CO_2 in seawater is difficult since the gas

not only dissolves but also reacts with water, forming compounds whose rates of dissociation are influenced by pH, temperature and salinity (Kutty 1968; Brett and Groves 1978). The weak base, ammonia, is the major excretory product of anchovy and its continual release during the experiment may affect the pH of the tank water, thus leading to a further source of error, since the method employed is very sensitive to the accurate measurement of the initial pH of the sample (Anderson and Robinson 1946). The active synthesis of fat tissue (Brett and Groves 1978) and the complete catabolism of amino acids such as histidine and glycine into CO_2, H_2O and NH_4 by ammonotelic fish (Brafield and Solomon 1972; Kutty and Mahomed 1975) could theoretically produce a RQ greater than unity.

Feeding activity accounted for a significant proportion of the carbon available in the ration (Table 2). The data supports the statement of Durbin *et al* (1981) that feeding frenzies are energetically less cost effective than the "normal" feeding behaviour and probably do not occur in the wild, except under exceptional circumstances when very high prey densities are encountered.

As during the experiments of Durbin *et al* (1981) satiation, which has been identified as an important aspect of the feeding behaviour and energetics of macrophagists (Ivlev 1961; Durbin 1979), appeared to be unimportant during the current experiments. None of the

fish displayed signs of ceasing to feed while food was being supplied to the tank. Durbin *et al* (1981) stated that microphagists such as the the menhaden and anchovy, which consume a continuous stream of small food particles rather than one large meal, probably do not become satiated since the plankton concentrations encountered in the wild are generally too low to saturate the handling and intestinal storage capacities of these fish, especially considering their rapid rates of digestion (Durbin and Durbin 1981; Chapter six). Durbin and Durbin (1981) found that 50% of the exogenous nitrogen excretion and faeces were released within 2 and 5.7 hours respectively after the midpoint of feeding. The rapid digestion and assimilation of the ration by microphagists has further implications. During both this study and that of Durbin *et al* (1981) no quantifiable effect of the Specific Dynamic Affect (SDA) was observed. There was no postfeeding peak in oxygen consumption associated with the SDA in macrophagists, which tend to have slower digestion rates (Muir and Niimi 1972; Pierce and Wissing 1974; Beamish 1974; Durbin *et al* 1981). The only possible evidence of the SDA was the differing elevations of the respiration rate vs swimming speed plots during particulate feeding and routine activity. However, the effect of any small fixed metabolic cost, such as the SDA is likely to be completely overshadowed by the continual variations in swimming activity during the feeding and postfeeding periods.

The present data are comparable to that collected for other

TABLE 5: Respiration rates of some clupeids during "resting" (routine), "active" and feeding activity states.

SPECIES	RESPIRATION RATE mg O_2/ g wet wt/ Hr				REFERENCE
	ROUTINE	ACTIVE	FILTER FEEDING	PARTICULATE FEEDING	
Engraulis capensis	0.111	0.282*	1.199	0.414+	This study
Sardinops caerulea	0.168	0.245		0.224	Lasker (1970); Blaxter and Hunter (1982)
Brevoortia tyrannus	0.270 0.100		0.470 0.480		Hettler (1976) Durbin *et al* (1981)
Clupea harengus	0.200 - 0.250				Aneer (1979)
Sardinops sagax	0.053	0.399			Villavincencio *et al* (1981)
Engraulis ringens	0.084	0.476			Villavincencio (1981)

* Highest routine measurement
+ Mean of all recorded feeding measurements

pelagic species (Table 5). Much of the variation between species can be attributed to differences in levels of activity and experimental design.

The log - linear relationships between respiration rate and swimming speed are consistent with other work reported in the literature (Wohlschlag 1957; Wohlschlag and Juliano 1959; Brett 1964; Brett and Sutherland 1964; Muir *et al* 1965; Durbin *et al* 1981). Brett (1964) discussed the validity of the metabolic rate - swimming speed relationship. The fits of the regressions could be improved by the use of a more sophisticated system to measure and analyse the swimming speeds, such as the TV and video system described by Gibson and Ezzi (1985). However, it must be realised that the behaviour of the fish during any activity will inevitably lead to variability; the more spontaneous the behaviour, the greater the variability. This is clearly demonstrated by the increasingly better fits to the data as one progresses from the postfeeding period when the fishes' behavior was most variable, through routine activity, particulate feeding to filterfeeding, when it was most consistent. Brett (1965) emphasised this point by stating that the fish must be pressed to maximum performance during experiments to provide the best fit between the oxygen consumption and swimming speed data, otherwise behavioural inputs could occur which would limit full metabolic expression.

It would appear that *E. capensis* has a larger metabolic scope

TABLE 6: The maximum swimming speeds recorded and derived respiration rates of anchovy during escape responses elicited by ten consequtive passes of an artificial predator (Wilson *et al* 1987). The respiration rates were calculated using the routine respiration rate - swimming speed regression.

PASS	MAX SWIMMING SPEED cm s^{-1}	CALCULATED RESPIRATION RATE mg O_2/ g wet wt/ Hr
1	61.98	1.098
2	57.31	0.848
3	82.60	3.431
4	71.77	1.886
5	79.38	2.871
6	90.10	5.193
7	66.67	1.423
8	80.46	3.048
9	89.52	5.029
10	83.21	3.548

than most of its planktivorous counterparts (Table 5), which in turn have larger scopes than less active species (Durbin *et al* 1981, Table 3). This fact is further emphasised when the respiration rates estimated from swimming speeds during escape responses elicited by an artificial predator (Wilson *et al* 1987) are considered (Table 6). Although these were the maximum speeds recorded during an escape response and swimming was not maintained at these levels for more than 10 - 15 seconds, the speeds did not show a significant reduction during the 10 consecutive passes of the predator silhouettes, suggesting that *E. capensis* is capable of sustaining these levels of activity for some time. It would be interesting to determine the maximum swimming speeds of *E. capensis* for comparison with other species (Brett 1964; Brett and Sutherland 1964; Hartwell and Otto 1978). The respiration rates appear to increase more rapidly in the Cape anchovy during feeding than in other species utilising the same feeding modes (Lasker 1970; Durbin *et al* 1981), indicating a greater metabolic cost. However, this may in part be due to the small size of the anchovy in relation to the pilchard and menhaden.

Unlike most other studies (Brett 1964; Brett and Sutherland 1964; Smitt 1965; Muir *et al* 1965; Muir and Niimi 1972; Durbin *et al* 1981) the measured routine respiration rates are lower than those predicted from respiration rate - swimming speed regressions during feeding or forced swimming activity. Brett (1964) and Smit (1965) stated that routine respiration rates would be greater

than predicted values due to the fish suffering from stress when unoccupied by some activity in the respirometer and because the spontaneous movements which characterise "resting" or routine activity are energetically more expensive than sustained motion. Observations during the present study showed that the fish, although excitable during routine activity, did not display the stressed behaviour such as "fluttering" and swimming nose first into the tank wall noted by Brett (1964) and Brett and Sutherland (1964) in their respirometer. The present data suggest that the size of the respirometer and the experimental design were less stressful and better suited to the fish than during other work, when individual fish were often confined to small containers (Brett 1964; Brett and Sutherland 1964; Lasker 1970). Also, routine respiration rates were recorded over a more extensive range of swimming speeds during this study than during many others (Brett 1964; Brett and Sutherland 1964; Lasker 1970; Durbin *et al* 1981).

The routine measurements collected during this study may be considered as a reflection of the oxygen consumption - swimming speed relationship of the anchovy during periods other than feeding and thus, are not analagous to the "resting" or routine measurements of other workers. This relationship is useful since it can be incorporated into carbon budget models and used to estimate the costs of nonfeeding activities such as migration and predator escape responses (Table 6). Many workers have extrapolated

respiration rate - activity relationships to zero activity to estimate a standard metabolic rate for use in comparisons between species (Beamish 1964; Brett 1964; Brett and Sutherland 1964; Durbin *et al* 1981; Villavincencio 1981). These are of limited ecological value since pelagic fish are never inactive, but continuously shift through a series of states involving feeding, horizontal movements and vertical migrations. Therefore a routine respiration rate - swimming speed relationship is more appropriate.

Although some studies have investigated the metabolic costs of filter and particulate feeding (Lasker 1970; Durbin *et al* 1981), the current work is unique in that it compares the costs of both feeding modes in one species. The most striking aspect of the data is that filtering is metabolically very expensive relative to particulate feeding (Inset Fig. 4). A 10 cm s^{-1} increase in swimming speed during filtering causes a 2.5 fold rise in oxygen consumption compared to a 1.67 fold increase during particulate feeding. This large difference, related to the dramatic increase in drag associated with prolonged mouth opening during filtering (Durbin *et al* 1981), between the metabolic costs of the two feeding modes has important trophic and energetic considerations.

James (Chapters two and four) demonstrated that particulate feeding was the dominant feeding mode and that the rates of ingestion of food were markedly higher during biting than filter-

ing. These findings, together with the oxygen consumption - swimming speed relationships, clearly indicate that *E. capensis* maximises its energy intake while minimising the metabolic cost. The high metabolic costs of filtering together with the relatively low feeding rates lend support to the hypothesis that this feeding mode may only be utilised by the fish in the wild when dense concentrations of microzooplankton and phytoplankton are encountered, as only under such conditions will the energy gain versus expenditure provide an acceptable return.

In conclusion, the dominant particulate feeding mode allows for the rapid, efficient intake of prey, while minimising the metabolic costs. The results of this study serve to emphasise the role of the anchovy as an opportunistic and efficient planktivore.

CHAPTER SIX

Nitrogen excretion and assimilation efficiencies of the Cape anchovy *Engraulis capensis* Gilchrist fed upon a variety of plankton diets.

Submitted to the Journal of Experimental Marine Biology and Ecology 1988

TABLE 1: Food type, ration size and feeding time during the experimental trials. Experiments 1 and 2 were preliminary trials.

EXP. No.	FOOD TYPE	SIZE mm	RATION SIZE mg dry wt./ g fish dry wt.	FEEDING TIME Hrs.
1	*Artemia salina*	2.360	72.70	1.0
2	*A. salina*	3.010	2.95	1.1
3	*Brachionus plicatilis*	0.567	66.69	2.0
	Paracalanus crassirostris	0.650		
4	*B. plicatilis*	0.256	12.46	3.0
	P. crassirostris	0.339		
5	*A. salina*	0.544	28.93	3.0
6	*A. salina*	0.911	111.10	3.0
7	Chaetoceros sp.	0.124	29.40	4.4
8	*Paracalanus* sp.	0.750	13.03	2.5
9	*A. salina*	2.460	20.54	3.0
10	*A. salina*	1.300	23.07	2.0
	P. crassirostris	0.620		
11	*Chaetoceros* sp.	0.114	18.86	5.5
12	*A. salina*	2.100	18.97	2.5
	Calanus finmarchicus	2.147		
13	*Cladocera*	2.501	11.41	2.0
14	*Cladocera*	2.480	23.50	3.0

INTRODUCTION

The Cape anchovy, *Engraulis capensis* (Gilchrist), is the mainstay of the South African and Namibian purse seine fisheries, with a combined total annual catch exceeding 600 000 tonnes. As part of an ongoing project to construct laboratory carbon and nitrogen budgets for *E. capensis*, previous work had determined the anchovys' diet and reviewed its trophic habits with respect to similar species worldwide (Chapters one and two) and related feeding behaviour to particle size, ingestion rates and energy expenditure (Chapters four and five). To complete the information needed to develop these budgets, data concerning the efficiency of utilisation of the ingested food and the losses incurred through defecation and excretion are required. A series of experiments were conducted to measure carbon and nitrogen absorption efficiencies and rates of faecal production and nitrogen excretion by anchovy fed a variety of diets. Preliminary data concerning the dynamics of digestive enzyme activity during and after feeding are also presented.

METHODS AND MATERIALS

Twelve experiments were conducted to investigate absorption efficiencies, faecal production and nitrogen excretion rates under controlled laboratory conditions. Details of the experimental treatments are shown in Table 1. Various zooplankters were fed to

the fish during 10 trials and *Chaetoceros* spp. was offered in a further two (Table 1). Six of the twelve trials (Exps. 3, 4, 8, 9, 12 and 14) also provided the oxygen consumption and swimming speed data discussed in Chapter five. Information regarding the maintenance of the fish in the laboratory, production of experimental foods and general experimental procedures are detailed in Chapters three, four and five.

Each experiment began with a measurement of the routine ammonium and urea excretion rates over 2 - 2.5 hours. Food was then supplied to the fish at a constant rate for a 2 - 5.5 hour period. Water samples for ammonium, urea and dissolved organic nitrogen (DON) were collected regularly during and for 20 - 24 hours and faeces for up to 45 hours after feeding. When considered necessary, the tank was flushed with filtered seawater immediately after the termination of feeding to reduce the level of ammonium in the water.

Enzyme Assays

During Exp. 12 single fish were removed at the initiation and termination of feeding (2.5 hrs), and at 10.5 and 24.75 hours after the initiation of feeding to assess the activity of four digestive enzymes: laminarinase, æ-amylase, protease and chitinase. The fish were separated from the rest of the school, removed with a hand net and immediately frozen. For the enzyme

analyses, the alimentary canal was dissected out of each fish and divided into four sections: the oesophagus, stomach, pyloric caeca and intestine. These sections were homogenised over ice in a glass tissue grinder in 15 ml 67 mM phosphate buffer pH 6.00 with 150 mM NaCl, centrifuged at 15 000 x g for 10 min and the supernatant decanted for enzyme assays. All assays were performed in triplicate. Protein content was assayed by the method of Lowry *et al* (1951).

Laminarinase was assayed using the method of Jacober *et al* (1980) using a substrate of 0.4% laminarin (Sigma). Aliquots of 250 µl enzyme extract which had been suitably diluted with phosphate buffer were added to an equal volume of laminarin and incubated in a shking water bath at 20°C for 0, 1 and 3 hours. Reducing sugars were measured at 660 nm using the Nelson - Somogyi method (Nelson 1952). Absorbance values were converted to "glicose equivalents" using the regression:

$$y = 0.03 + 17.14x \quad (N = 25,\ r^2 = 0.95)$$

where y = absorbance at 660 nm; x = mg glucose. æ - amylase was also assayed by the Nelson - Somogyi method using 0.5% oyster glycogen as a substrate.

Chitin substrate was prepared by the method of Reichenbach and Dworkin (1981). Ten g powdered crab shell chitin (Sigma) was treated with 100 ml cold concentrated HCl for 1 hour. The chitin was then precipitated by pouring the solution into 1 l distilled

water at 4°C whilst stirring vigourously. The precipitate was collected by filtration onto a Whatman GF/C filter and dialysed overnight against running tap water. The pH was then adjusted to 7.0 with 1 N KOH and the resultant slurry autoclaved without allowing complete drying. Aliquots of 250 µl of enzyme preparation were added to an equal volume of the chitin slurry (20.3 mg. ml^{-1} dry wt.) with 50 µl toluene to inhibit bacterial activity (Okutani 1966) and the mixture incubated in a shaking water bath for 0, 1, 24 and 96 hours at 20°C. The replicates were assayed for the chitinase end product β-1,4 linked N-acetylglucoseamine (NAG) according to the method of Reissig *et al* (1955; see also Monreal and Reese 1969) using a wavelength of 585 nm. Chitinolytic activity was expressed as mg NAG (Sigma) fron the calibration regression:

$$y = 0.06 + 30.55x \quad (N = 11,\ r^2 = 0.99)$$

where y = absorbance at 585 nm; x = mg NAG.

Protease was measured after the method of Long *et al* (1981) using 0.5% Azocaesin (Sigma) in 0.2 M Tris - HCl pH 7.8 as substrate (see Reimerdes and Klostermeyer 1976 for substrate suitability). 250 µl enzyme was added to 500 µl of azocaesin substrate and incubated in a shaking waterbath at 20°C for 0, 1 and 3 hours. The reaction was stopped by the addition of 1 ml 10% trichloracetic acid and the vials were held at 5°C for 30 min. The precipitate was then sedimented by centrifugation and 1 ml of the supernatant added to 1 ml 1 N NaOH. The acid soluble azopeptides were measured spectro-

photometrically at 440 nm.

All data are expressed in terms of end product. mg protein homogenate^{-1}. hr^{-1}.

Faeces Collection

Faeces were siphoned into a clean 20 l bucket at 1 - 8 hour intervals. The water removed from the tank with the faeces was returned by back filtration and the faeces rinsed in distilled water, transferred to preweighed aluminium dishes, dried for 24 hours at 60°C and weighed. Each batch was subsampled for carbon and nitrogen (3 - 5 replicates) and ash weight (3 subsamples). Total carbon and nitrogen were measured using a Heraeus Rapid CHN Analyser.

Absorption Efficiencies

Two methods were used to estimate absorption efficiencies, both of which depended upon the assumption of quantitative recovery of the faecal material. Overall dry weight, carbon and nitrogen absorption efficiencies were calculated from the total amounts of each constituent in the faeces and that available in the food using the following expression: 1

$$\%\text{Absorption Efficiency} = \frac{\text{COMPONENT}_{food} - \text{COMPONENT}_{faeces}}{\text{COMPONENT}_{food}} \times 100$$

In the second method, the carbon and nitrogen absorption efficiencies were calculated for each batch of faeces collected. The ash weight of the food and faeces never differed by more than 5.0 % (Table 2) and therefore the ash weight of the faeces was used as a tracer to estimate the proportion of the total ration consumed by the fish that corresponded to the amount of faeces produced. Using carbon and nitrogen data of the food, the amount of these elements in the estimated ration consumed could be back calculated and the absorption efficiencies then calculated using equation 1.

Nitrogen Excretion

Water was collected in a 100 ml acid washed syringe and filtered through prerinsed glass fibre filters into a clean acid washed beaker. Triplicate 5 ml subsamples for analyses of ammonia, urea, and DON were stored in clean, disposable testtubes at -10°C until processed. Ammonium and urea concentrations were determined in triplicate according to the methods described in Grasshoff (1976) scaled down to a sample volume of 5 ml.

All N data presented in this paper are expressed as per gram fish dry weight.

TABLE 2: Chemical composition of fish, food and faeces.

	DRY WT. AS % WET WT.	COMPOSITION AS % DRY WT. C	N	ASH	C:N RATIO
Engraulis capensis	32.01	52.52	14.97	17.91	4.43:1

EXP No.	CHEMICAL COMPOSITION (as % food dry wt) FOOD C	FOOD N	FAECES C	FAECES N	ASH WEIGHT FOOD mg	FAECES mg	% DIFFERENCE	CHEMICAL COMPOSITION (as % elemental composition of fish) DRY WT.	C	N
3	41.01	8.76	15.49	2.30	529.23	536.33	1.34	6.67	5.21	3.90
4	34.75	7.44	12.41	1.37	163.24	166.44	1.96	1.25	0.82	0.62
5	44.19	8.99	4.02	0.69	124.18	124.24	0.05	2.89	2.43	1.74
6	42.51	8.77	5.33	0.99	472.42	455.62	3.56	11.11	8.99	6.51
7	16.42	3.16	8.20	0.57	114.74	117.85	2.71	2.94	0.92	0.62
8	43.87	7.94	2.10	0.39	102.49	105.97	3.40	1.30	1.09	0.69
9	18.89	4.42	5.10	0.31	133.62	137.25	2.72	2.05	0.74	0.61
10	35.18	7.42	10.34	1.09	166.82	168.75	1.16	2.31	1.54	1.14
11	14.81	2.78	7.25	0.43	101.36	99.59	1.75	1.89	0.53	0.35
12	43.07	10.53	4.74	0.59	396.84	408.30	2.89	1.90	1.56	1.33
13	48.18	10.88	9.92	1.11	259.68	247.14	4.83	1.14	1.05	0.83
14	48.14	10.80	9.92	1.35	480.62	493.98	2.78	2.35	2.15	1.67

RESULTS

It was assumed that each of the fish in the school consumed an equal portion of the available ration and contributed equally to the nitrogen excretion and faecal production during the experiments. Experiments 1 and 2 were preliminary trials and the data has been omitted from all analyses.

The fish were fed rations ranging from 11.41 mg - 111.10 mg food dry weight/ g fish dry weight, corresponding to 1.14 % to 11.11 % dry body weight over a 2 - 5.5 hour feeding period (Table 1). The chemical compositions of the fish, food and faeces are summarised in Table 2.

Enzyme Activity

The data suggest that there is an induction of digestive enzyme activity after the onset of feeding which reaches a peak after the ingestion of food is complete and then declines to prefeeding levels as the undigested remains of the ration are eliminated (Fig 1). The increase in æ-amylase activity (between t = 2.5 hrs to t = 10.5 hrs) lagged behind the increases of the other enzymes (t = 0 hrs to t = 2.5 hrs).

Laminarinase activity increased rapidly during feeding to a peak at t = 2.5 hrs and thereafter declined approximately exponentially

FIGURE ONE : Time courses of enzyme activities in the alimentary tracts of Cape anchovy sampled during Experiment 12.

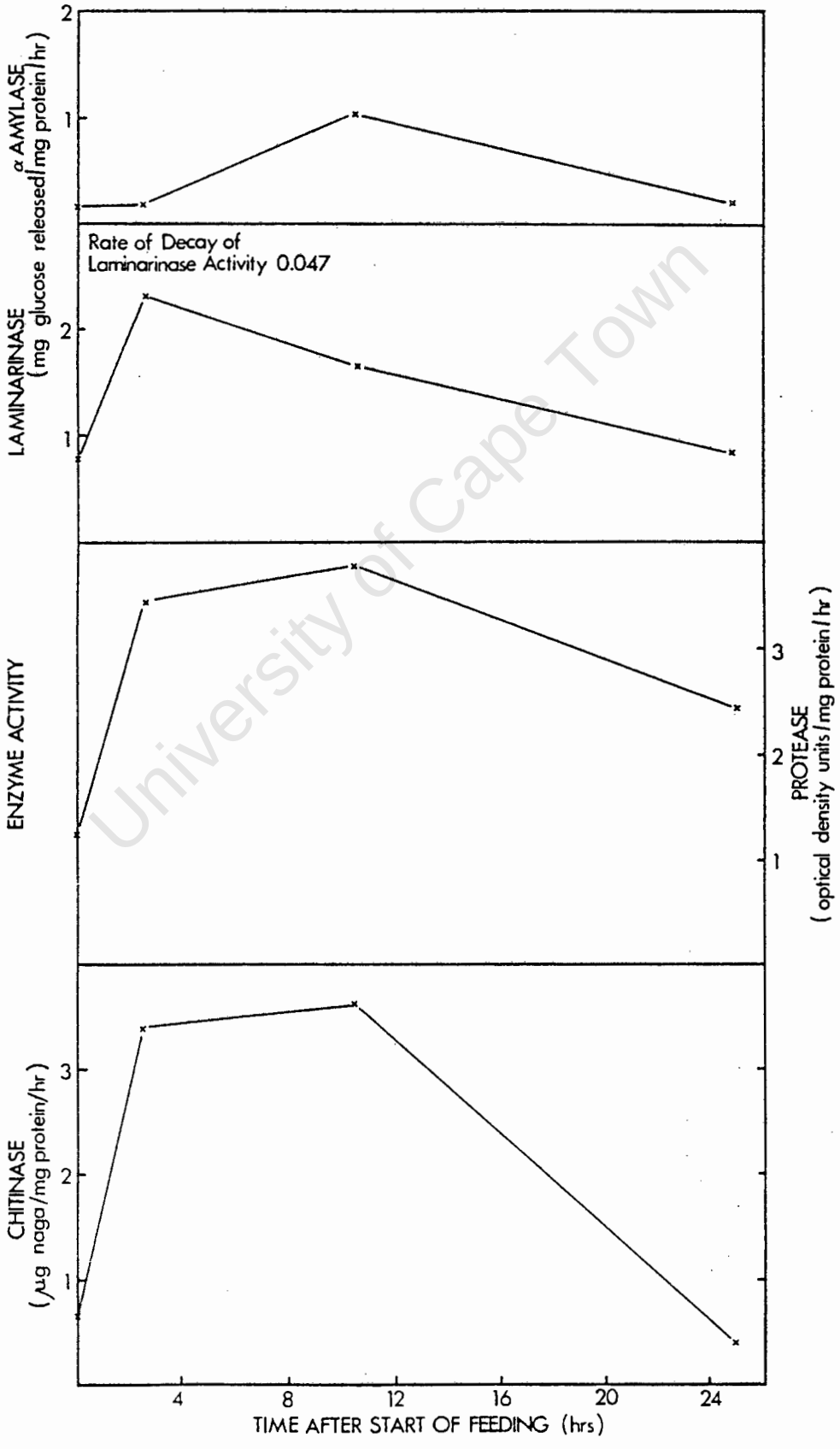


TABLE 3: Distribution of Enzyme Activity in the alimentary tract of anchovy during and after feeding.

ENZYME	TIME Hrs	% OF TOTAL ENZYME ACTIVITY IN WHOLE ALIMENTARY TRACT OESOPHAGUS	STOMACH	CAECA	INTESTINE
AMYLASE	0	-	-	66.5	33.5
	2.5	-	-	72.0	28.0
	10.5	-	2.6	51.8	45.6
	24.75	-	52.1	35.9	12.0
LAMINARINASE	0	15.1	37.5	30.4	17.0
	2.5	1.2	53.4	31.5	13.9
	10.5	9.1	15.3	53.5	22.1
	24.75	47.8	21.9	19.4	10.9
PROTEASE	0	41.0	-	52.3	6.7
	2.5	22.5	9.9	40.4	27.2
	10.5	23.4	10.8	45.0	20.8
	24.75	34.5	48.9	16.6	-
CHITINASE	0	-	-	10.0	90.0
	2.5	-	74.1	1.1	24.8
	10.5	16.3	33.4	22.7	27.6
	24.75	-	-	-	100.0

to prefeeding levels at t = 24.75 hrs at a rate similar to the faecal production rate for this experiment (Fig. 2). The main portion of this enzyme's activity shifted from the stomach and caeca during and immediately after feeding (t = 0 hrs and t = 2.5 hrs), to the caeca (t = 10.5 hrs) and oesophagus (t = 24.75 hrs, Table 3).

Protease and chitinase both showed rapid increases in activity after the initiation of feeding, which were sustained until t = 10.5 hrs, after which activity declined. Protease activity was generally greatest in the oesophagus and caeca, although its activity was concentrated in the stomach at t = 24.75 hrs (Table 3). Chitinase activity shifted from the intestine (t = 0 hrs) to the stomach (t = 2.5 hrs), became evenly distributed throughout the alimentary canal (t = 10.5 hrs) before becoming concentrated in the intestine again (t = 24.75 hrs, Table 3).

Faeces Elimination

Faeces produced by the anchovy generally formed cohesive, dark coloured cylinders surrounded by a thin, translucent mucous sheath and were easily detected against the the pale blue background of the tank bottom. Faeces produced from zooplankton diets were either red - brown or dark brown in colour, whilst those resulting from a phytoplankton diet were green - brown with a more obvious mucous sheath. Faeces began to appear 0.89 ± 0.29 hrs

FIGURE TWO : The faecal elimination rates of anchovy during and after a 2 - 3.5 hour feeding period. The heavy bars on the X - axis indicate the duration of the feeding period and the arrows define the period of exponential decline in the faecal elinination rates.

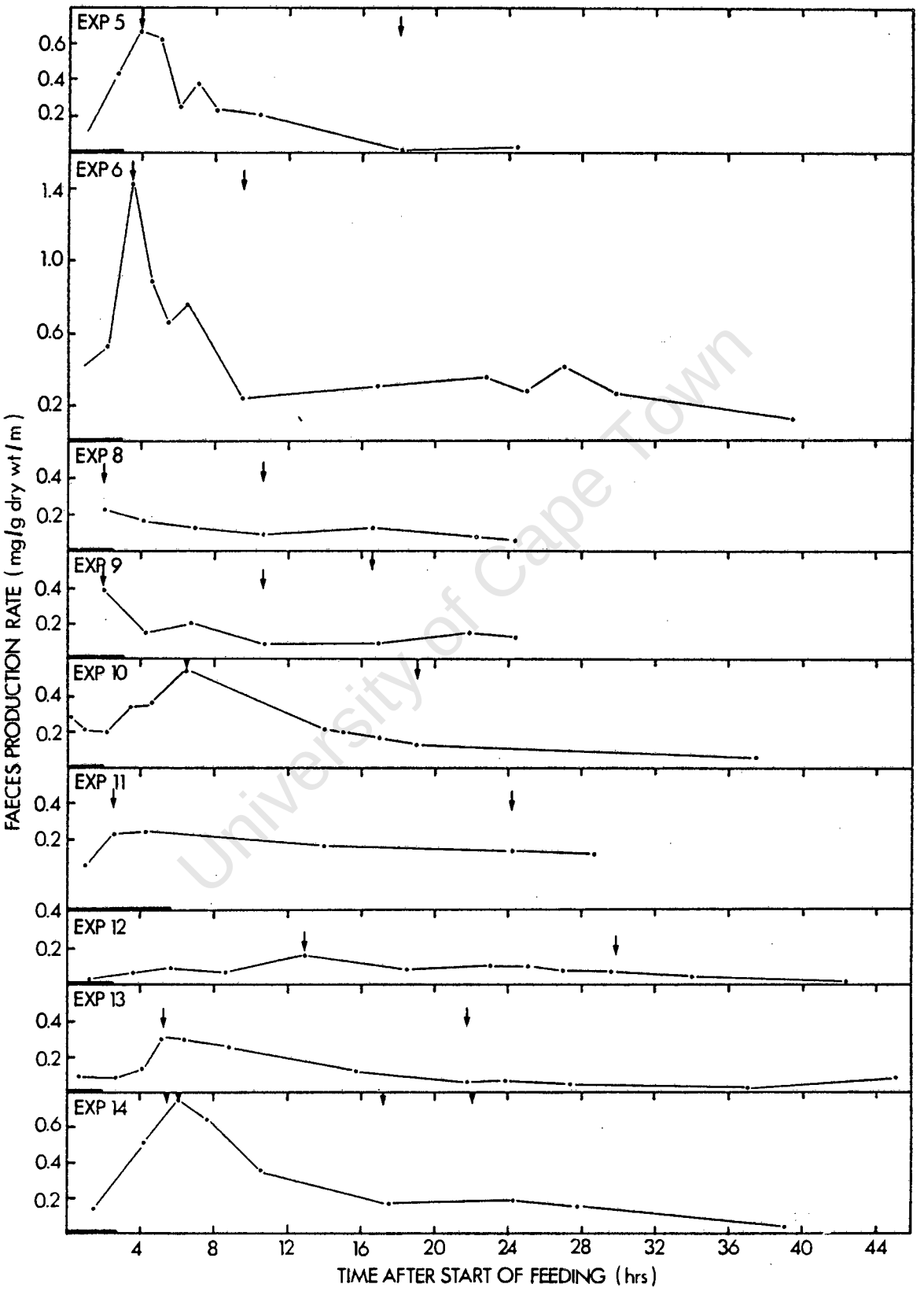


TABLE 4: Faeces elimination and nitrogen excretion of anchovy in relation to the 2 - 5.5 hour feeding periods.

EXP. No.	TIME (Hrs) t_o	$t_{o.5}$		t_1		RATE OF EXPONENTIAL DECLINE IN ELIMINATION RATE (Hr^{-1})#	% ASH WT COLLECTED DURING NON - EXPONENTIAL PHASE
	Elimination began	50% ash eliminated	50% N excreted	90% ash eliminated	90% N excreted		
5	0.83	3.83	1.70	8.39	3.01	-0.259	0.29
6	0.65	13.86	1.79	32.54	6.40	-0.272	66.27
8	1.25	8.41	3.41	17.95	5.22	-0.085	40.51
9	1.30	7.27	0.85	19.89	1.04	-0.150	39.66
10	0.21	11.55	1.88	34.15	4.85	-0.107	17.97
11	0.75	11.81	0.72	21.71	1.98	-0.025	14.84
12	1.00	16.89	1.41	33.40	2.81	-0.058	15.38
13	0.75	9.77	1.70	28.67	2.22	-0.103	18.67
14	1.25	9.00	2.97	26.21	7.15	-0.135	23.44
MEAN ± 95%C.L.	0.89±0.35*	11.07±2.64*	1.83±0.74	26.82±5.35*	3.85±1.77		

Exponential decline of elimination rate calculated from the peak rate to end of the experiment; e.g. in Exp 5 from t = 4 hrs onwards (Fig 2).

after the initiation of feeding activity and 24 hrs to 48 hrs were required to completely eliminate the remains of a meal (Fig. 2 and Table 4). Faecal elimination generally increased from an initial low rate to a peak after the termination of feeding. It then declined exponentially for 6 - 20 hrs, after which elimination continued at a low, constant rate for the duration of the experiment (Fig 2). The time taken to eliminate 50% and 90% of the ash content of the ration varied over a wide range and bore little relation to ration type and size or feeding time (Table 4). The ash weight of the faeces collected during the period of non-exponential, constant elimination over the latter period of the experiments accounted for 0.29% to 66.27% of the total ash weight of the ration (Table 4).

Variation in faecal elimination rates existed even when the same food type was offered. This may have been due to differing food sizes, but was probably due to the variations in the physiological status of the fish during different experiments. During Exp. 11 the faecal elimination rate began to decline before the end of the feeding period, indicating that the ingestion rate of food was lower than the elimination rate. This fact could have led to an underestimate of the exponential coefficient, since food was still being ingested at a low rate at the beginning of the period of exponential decline.

FIGURE THREE A : Changes in the carbon and nitrogen absorption efficiences, faeces elimination rates and the C:N ratios of the faeces during the experimental time couses when zooplankton was offered as food. Experiments 3 and 4 are ommitted due to the lack of adequate data.

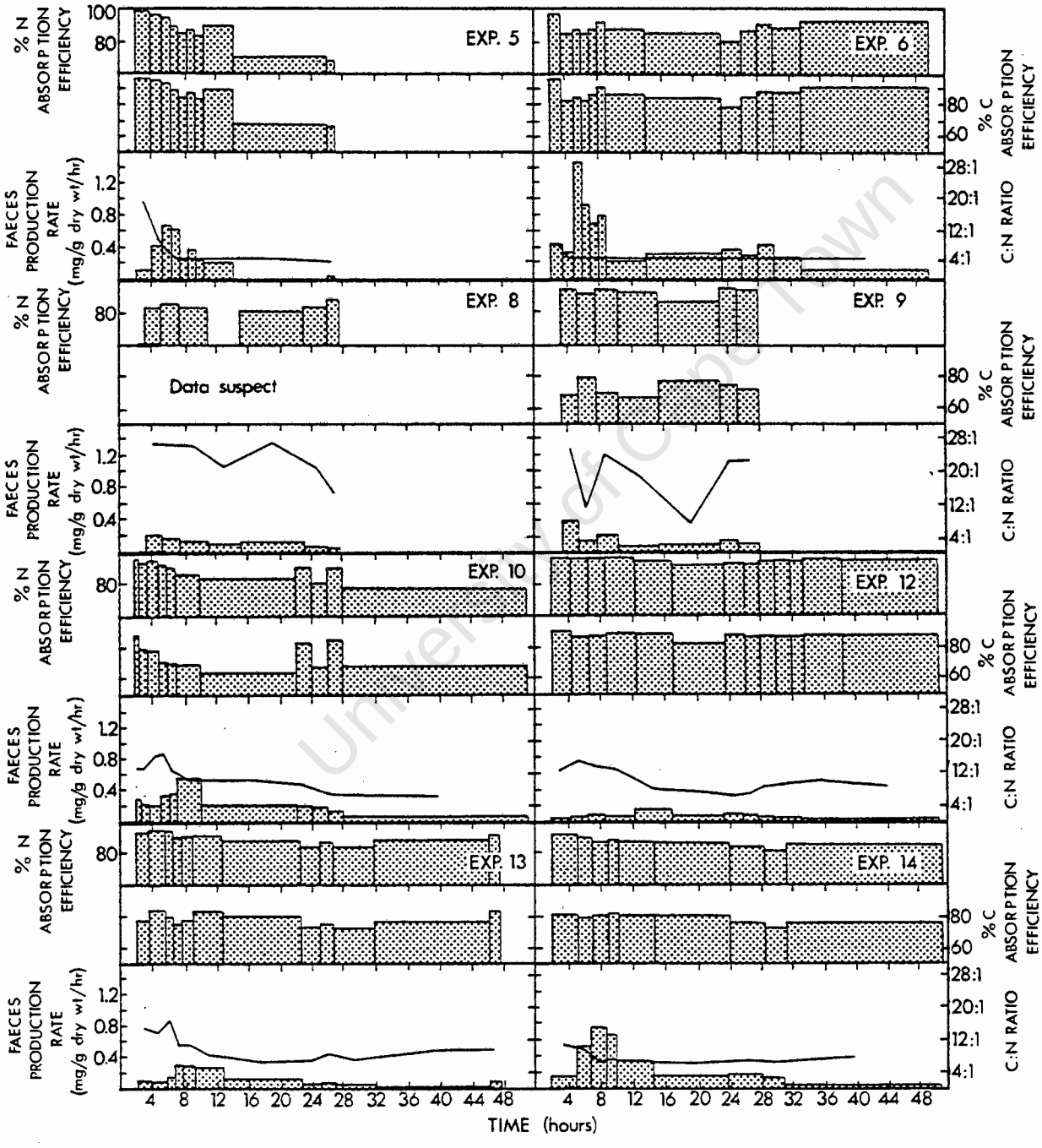


TABLE 5: Overall dry weight, C and N assimilation efficiencies of zooplankton and phytoplankton diets by *E. capensis*.

FOOD TYPE	EXP N°	RATION SIZE mg/ g dry wt	ASSIMILATION EFFICIENCIES % DRY WT	CARBON	NITROGEN
ZOOPLANKTON	3	66.69	63.88	62.24	73.75
	4	12.46	62.03	64.28	85.54
	5	28.93	86.17	90.90	92.35
	6	111.10	87.10	87.47	88.72
	8	13.03	71.90	82.49	83.30
	9	20.54	82.80	72.98	93.06
	10	23.07	52.55	70.60	85.30
	12	18.97	82.30	89.01	94.35
	13	11.41	62.37	79.41	89.81
	14	23.50	62.38	79.40	87.59
MEAN ± 95 % CL			71.35±8.85	77.88±7.22	87.38±4.28
PHYTOPLANKTON	7	29.40	68.64	50.08	81.94
	11	18.86	74.02	51.05	84.48
MEAN ± S.D.			71.33±3.80	50.57±0.69	83.21±1.80

Absorption Efficiencies

The mean dry weight absorption efficiency was almost identical for zooplankton and phytoplankton (Table 5). The mean carbon absorption efficiency for zooplankton was significantly greater than that for phytoplankton (Table 5, t_{sample} = 8.56; $t_{0.0005(1),7}$ = 4.781, $P < 0.0005$). The wide variation in the carbon absorption efficiency within the zooplankton data seemed to be related to diet. Rations containing *Brachionus plicatilis* and *Paracalanus crassirostris* resulted in the lowest zooplankton carbon absorption efficiencies, whilst *A. salina* and the larger copepods produced higher values.

Mean nitrogen absorption efficiencies were high and similar for zooplankton and phytoplankton diets (Table 5) and always exceeded the corresponding carbon efficiencies. There was less variation in the nitrogen absorption efficiencies within the zooplankton data and it did not appear to reflect differences in diet, although the lowest value recorded still resulted from a diet of *B. plicatilis* and *P. crassirostris* (Table 5).

Absorption efficiencies did not mirror the reductions of the faecal elimination rates after feeding ceased, but remained approximately constant throughout the experiments (Fig. 3a). The C:N ratios, on the other hand, declined during most of the experimental time courses (Fig. 3a). Exps. 5, 10 and 11 differed

FIGURE THREE B : Changes in the carbon and nitrogen absorption efficiencies, faeces production rates and the C:N ratios of the faeces during the time couse of experiment 11 when phytoplankton was offered as food.

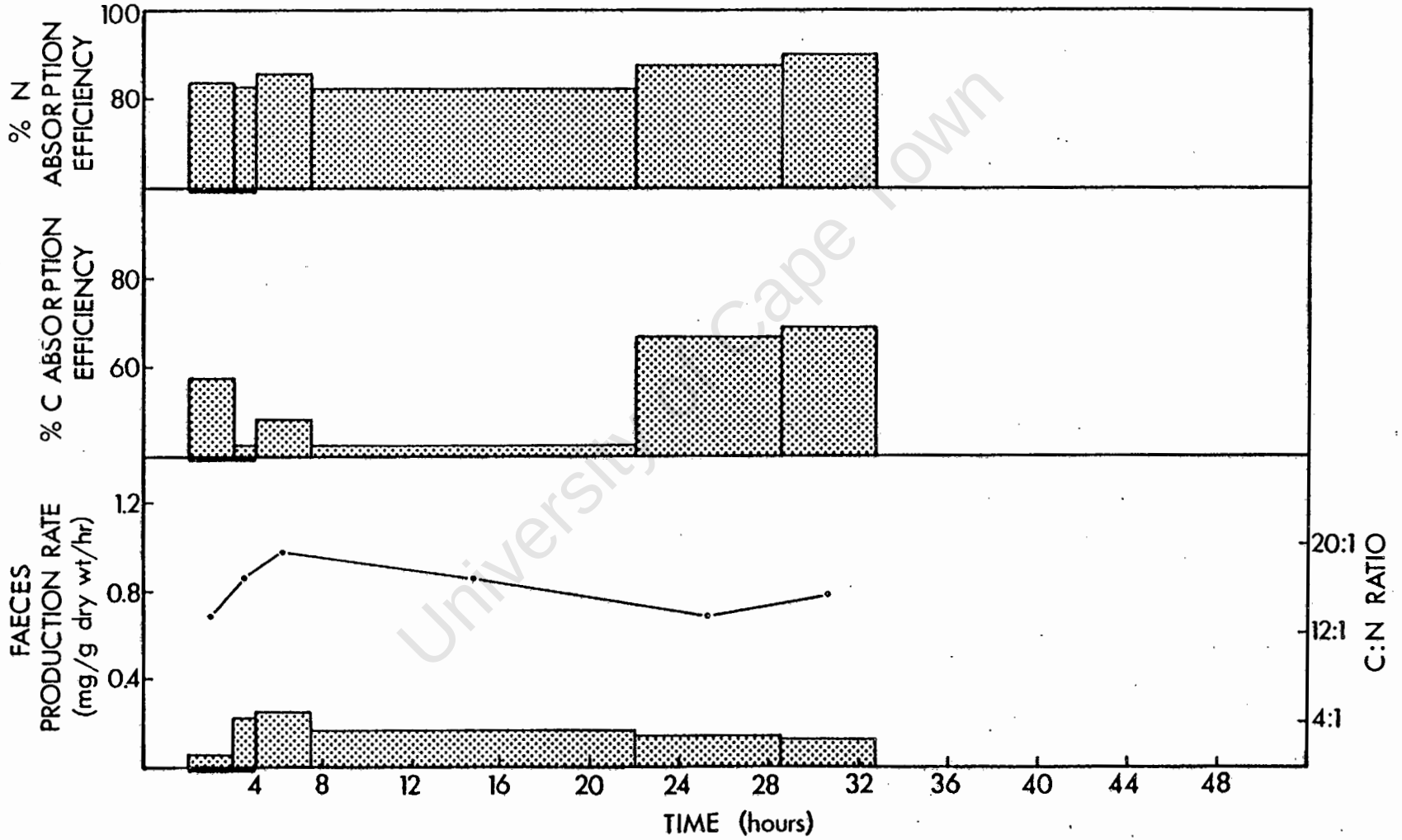
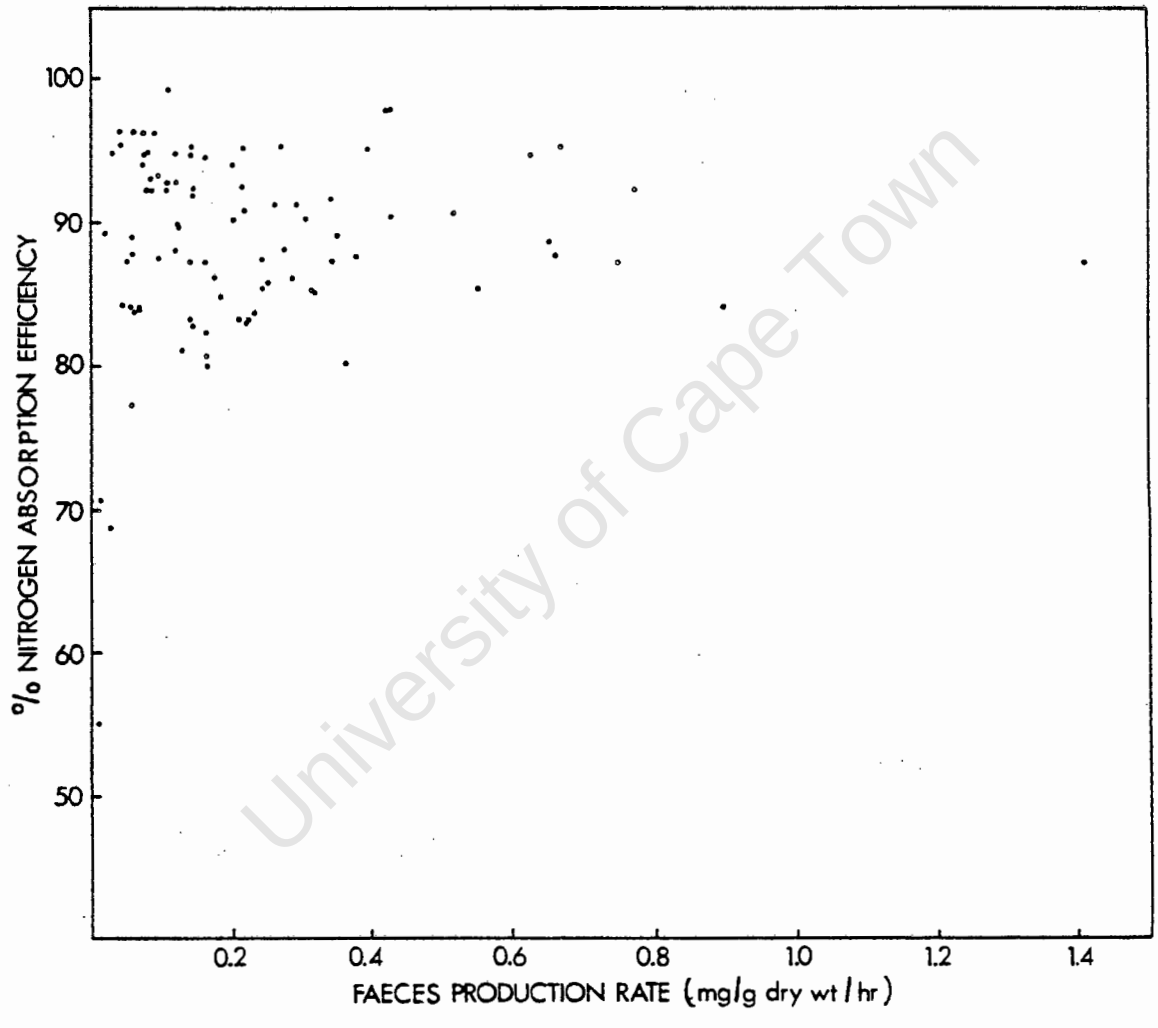


FIGURE FOUR : The relationship between the faecal elimination rate and the nitrogen absorption efficiency.



from this trend. In the former two trials, the absorption efficiencies decreased during the time courses, while in the latter the efficiencies increased at the end of the trial (Fig 3a and 3b). The C:N ratios declined most precipitously during Exps. 5 and 10 (Fig. 3a) when there were copious mucous strands associated with the faeces in the latter stages of these two experiments. No relationship was apparent between the faecal elimination rate and the nitrogen absorption efficiency (Fig. 4).

Nitrogen Excretion

The large changes in the concentration of ammonia during experiments meant that its excretion rate could always be measured satisfactorily. However, due to the small changes in urea and dissolved organic nitrogen (DON) concentrations in the tank, together with the inherently greater errors in the methods used to assess these compounds, it was often difficult to accurately determine their excretion rates. To overcome this problem fish were confined to 5l and 10l containers on several occasions to determine their excretory products in a manner similar to that described by McCarthy and Whitledge (1972). Although more accurate determinations of urea and DON resulted, the fish were extremely stressed and died after 1 - 2 hours of confinement. The data were not considered to be suitable for the present study and have been discarded. Instead, the total organic nitrogen

FIGURE FIVE : The rates of ammonia and urea excretion by the Cape anchovy before, during and after being fed A) high, B) medium and C) low rations of zooplankton.

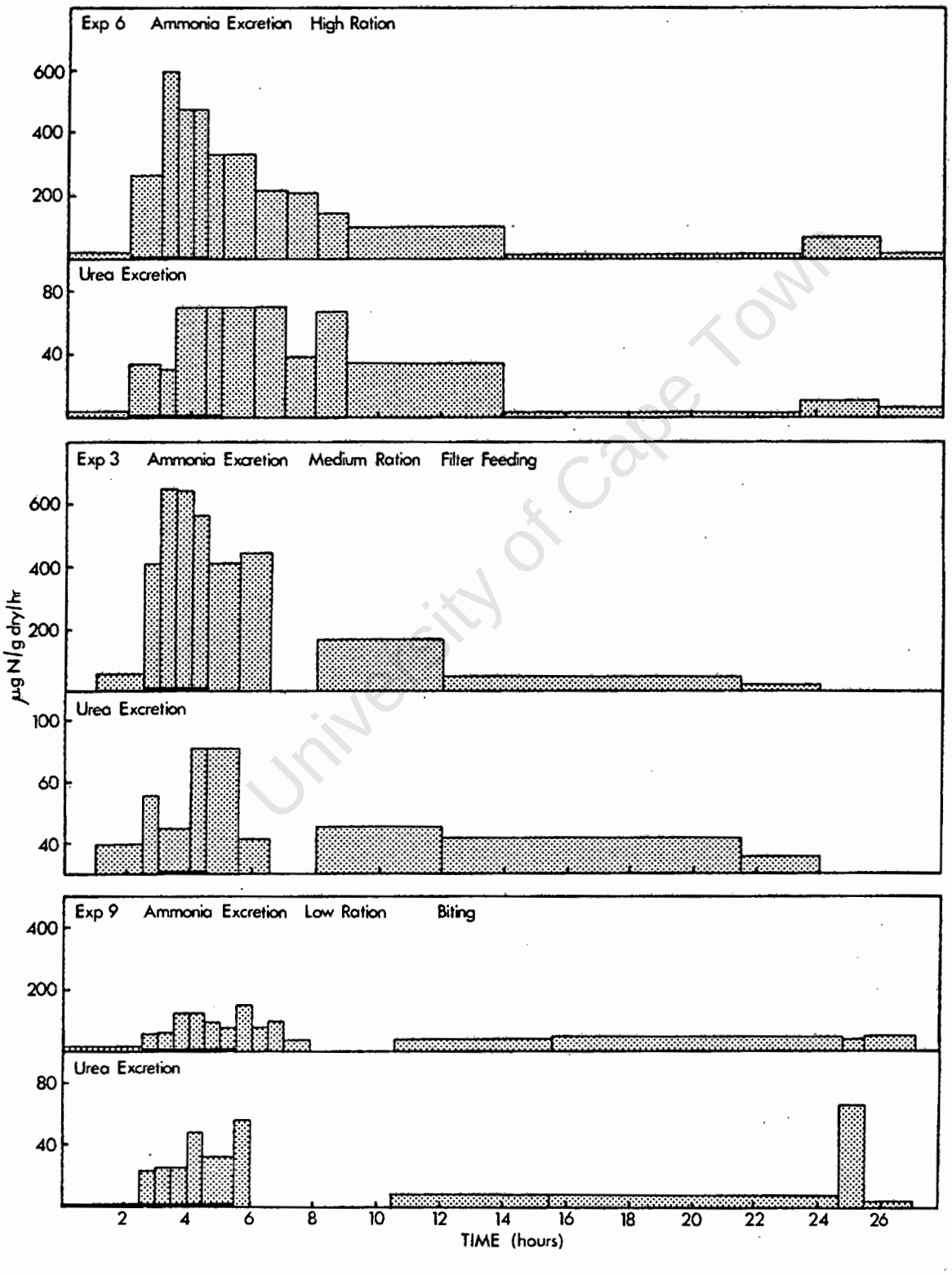
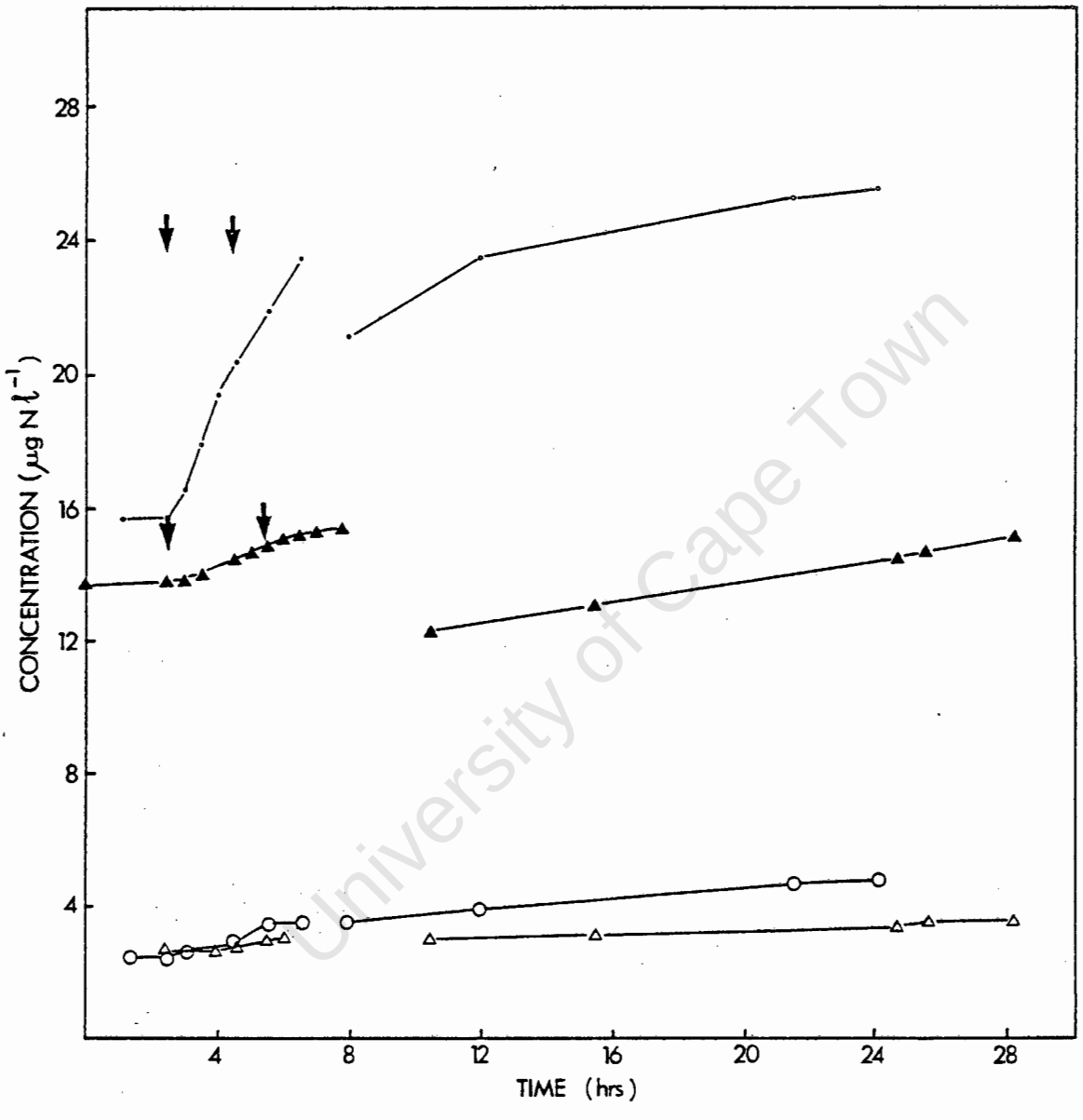


FIGURE SIX : The absolute changes in ammonia and urea concentrations in the tank due to excretion by the Cape anchovy before, during and after feeding. The data for medium (Exp. 3) and low (Exp. 9) ration experiments are shown.



excretion was estimated using the DON : NH_4 ratio of 0.437:1 determined by Durbin and Durbin (1981) for feeding *Brevoortia tyrannus*. All NH_4 excretion rates have been corrected accordingly.

The mean routine (endogenous), NH_4 excretion rate ± 95% C.L. for all experiments was 24.31 ± 4.32 µgN. g dry wt^{-1}. hr^{-1}. Using Durbin and Durbin's (1981) correction for organic excretion, this is equivalent to a total N excretion rate of 34.93 ± 6.21 µgN. g dry wt^{-1}. hr^{-1}.

Total exogenous N (N from the ration) was calculated by subtracting the endogenous (routine N excretion) rate of 34.93 µgN. g dry wt^{-1}. hr^{-1} from the N excreted during the period of elevated excretion; defined as the period of time during which excretion exceeded the upper one standard deviation of the mean non feeding rate (34.93 ± 16.92 µ N. g dry wt^{-1}. hr^{-1}).

Nitrogen excretion followed a similar format during all experiments, regardless of food type, ration size or feeding time (Fig. 5). Excretion increased above the non feeding rate within 30 minutes of the initiation of feeding and declined immediately after its termination (Fig. 5). The peak in urea excretion rates lagged behind those of NH_4 by ± 1 - 1.5 hours (Fig. 5). Increases in NH_4 and urea in the tank water were rapid and approximately linear during the feeding period (Fig. 6).

FIGURE SEVEN : The relationships between the ingested ration (R_n) and A) total exogenous excretion (e_n) and B) the total daily nitrogen excretion (E_n). The 95% confidence limits are shown.

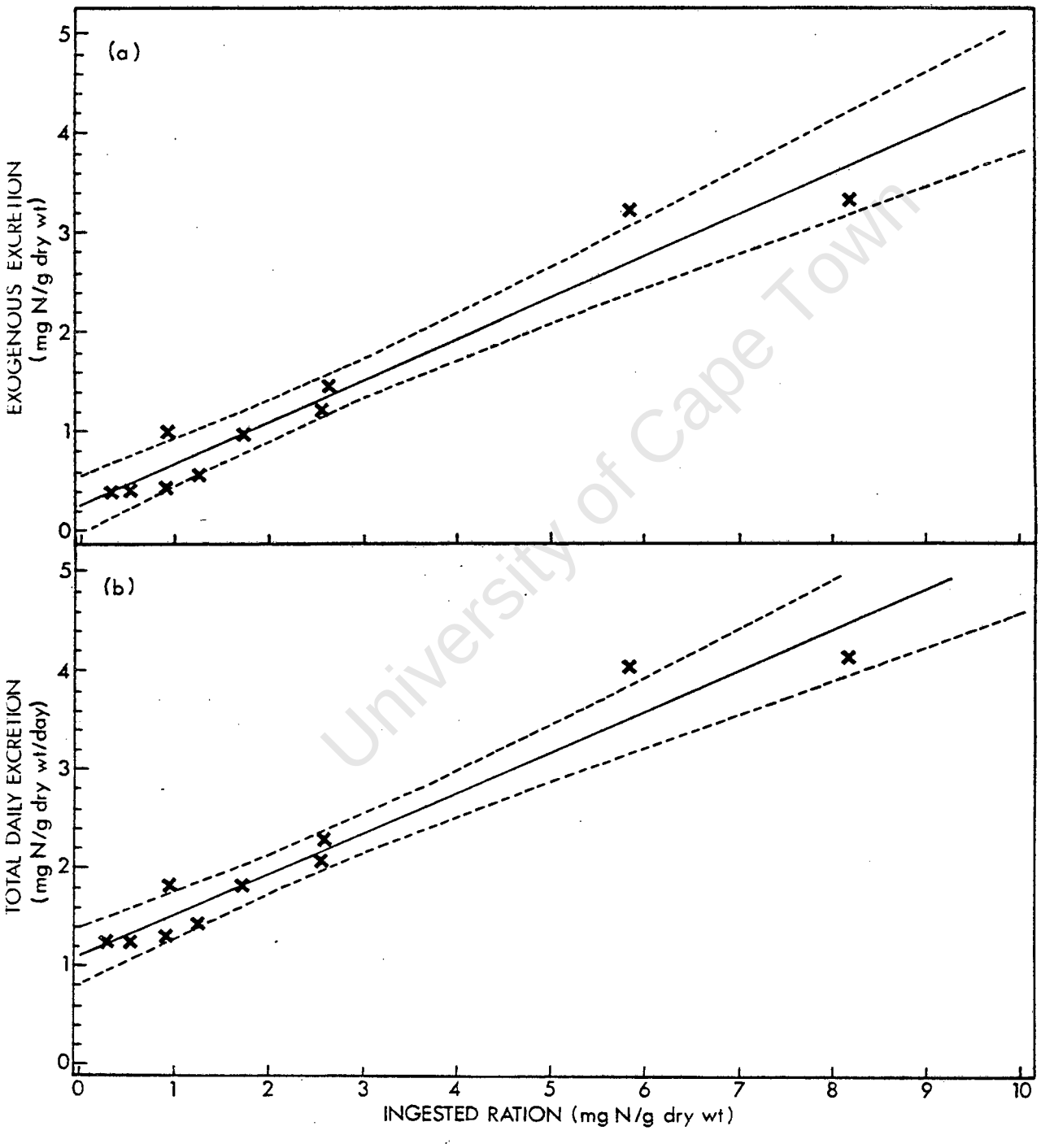
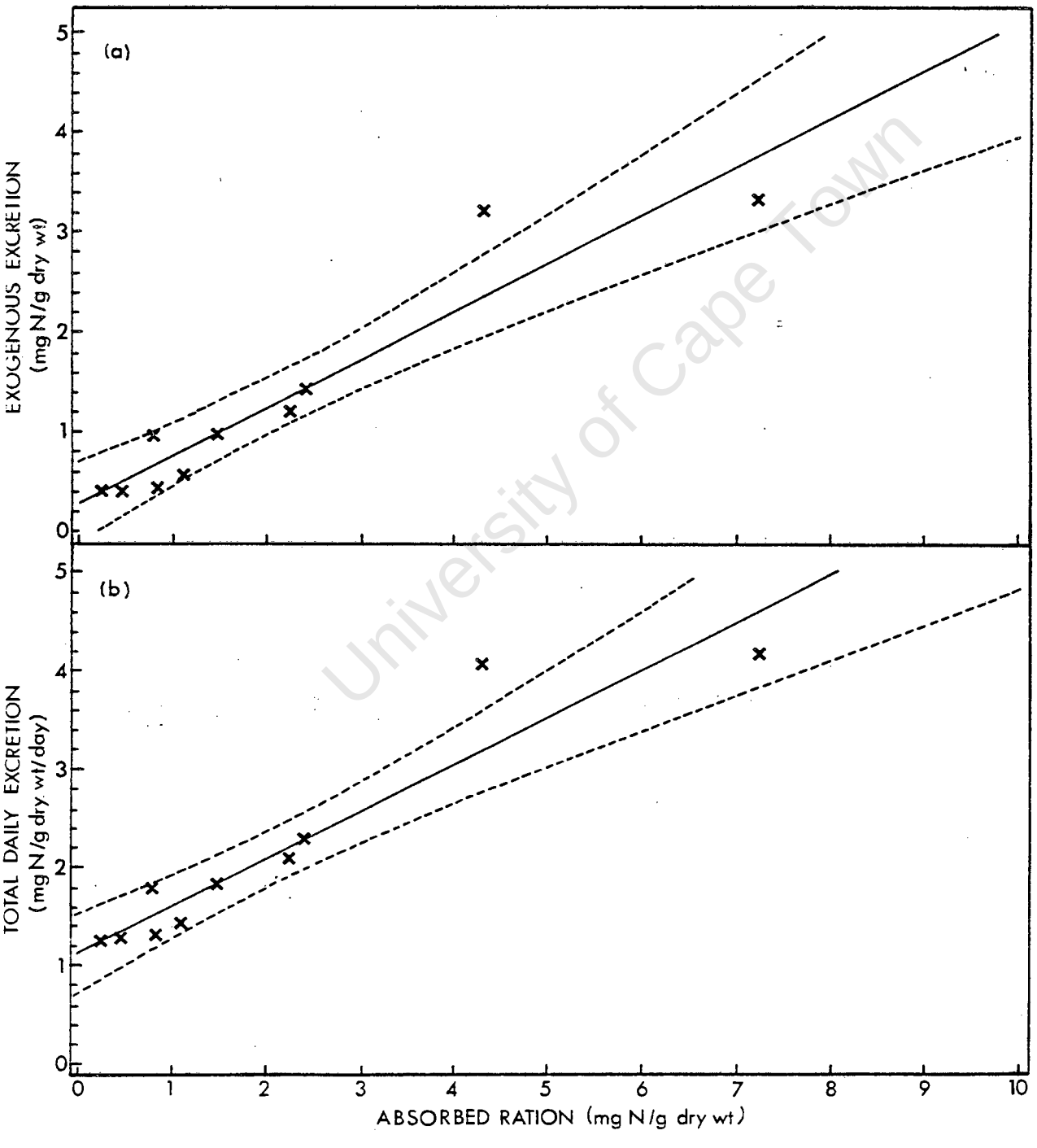


FIGURE EIGHT : The relationship between the absorbed ration and A) total exogenous excretion (e_n) and B) the total daily excretion by the anchovy (E_n). The 95% confidence limits are shown.



The absorption and subsequent excretion of dissolved nitrogen from the ration was considerably more rapid than the elimination of the meal; 50% of the absorbed nitrogen was excreted in 1.83 ± 0.74 hours after the midpoint of feeding and 90% had been excreted within 4 hours of the end of the feeding period (Table 4). Excretion rates returned to non feeding levels within 6 hours of the end of feeding.

Significant relationships exist between the total exogenous N excretion (e_N) and both the total N in the ingested (R_N) and absorbed (pR_N) rations for all experiments (Figs. 7a and 8a). The least squares linear regressions are :

$$e_N = 0.273 + 0.415\ R_N \text{ mgN. g dry wt}^{-1} \quad (2)$$

and

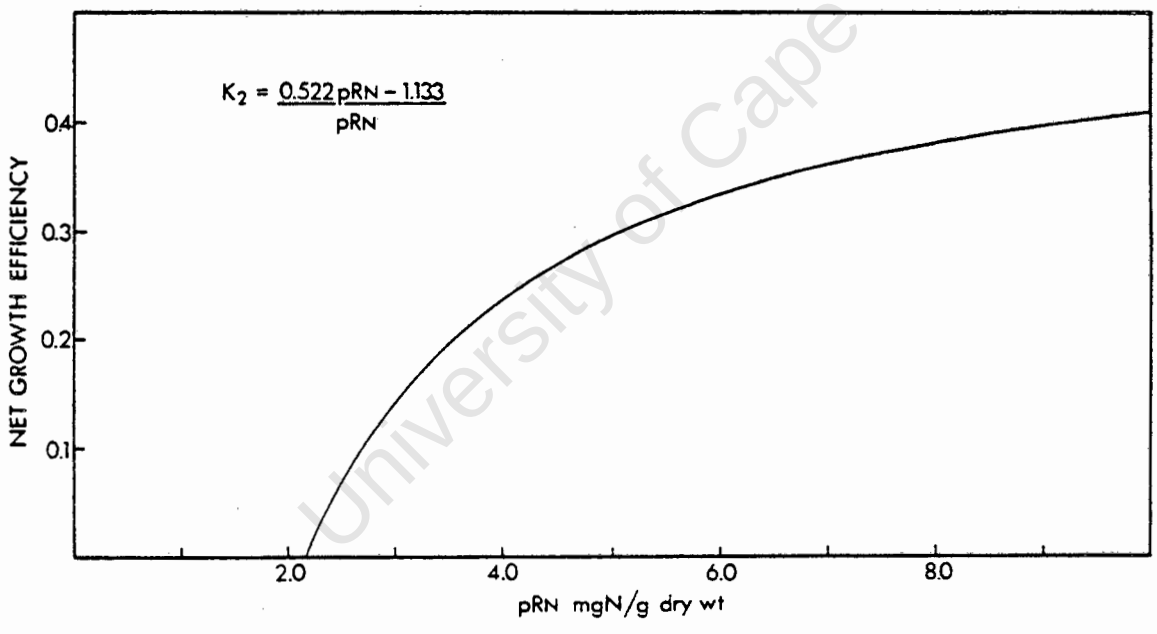
$$e_N = 0.295 + 0.478\ pR_N \text{ mgN. g dry wt}^{-1} \quad (3)$$

p is the N absorption efficiency.

Thus, *E. capensis* retained 58.5% of the ingested N and 52.2% of the absorbed N for growth; the rest (41.5% R_N and 47.8% pR_N), being in excess of immediate requirements, was excreted.

These relationships may be expressed in terms of total daily N excretion (E_N) by incorporating the daily endogenous excretion; 0.838 mg N. g dry wt^{-1}. day^{-1} (Fig. 7b and 8b). The regressions

FIGURE NINE : The calculated net growth efficiency (K_{2n}) of Cape anchovy for nitrogen as a function of the absorbed ration.



of E_N against R_N and pR_N respectively are:

$$E_N = 1.112 + 0.415\ R_N \quad \text{mgN. g dry wt}^{-1}\text{. day}^{-1} \qquad 4$$

and

$$E_N = 1.133 + 0.478\ pR_N \quad \text{mgN. g dry wt}^{-1}\text{. day}^{-1} \qquad 5$$

The latter relation can be employed to calculate the daily growth of the anchovy in nitrogen (G_N) and hence net growth efficiency (K_{2N}):

$$G_N = pR_N - E_N$$

$$= pR_N - (1.133 + 0.478\ pR_N) \qquad 6$$

$$= 0.522\ pR_N - 1.133 \text{ mgN. g dry wt}^{-1}\text{. day}^{-1} \qquad 7$$

$$K_{2N} = \frac{G_N}{pR_N} \qquad 8$$

$$= \frac{0.522\ pR_N - 1.133}{pR_N} \qquad 9$$

K_{2N} values for different ration sizes are shown in Fig. 9. For zero net growth, i.e. no gain nor loss in nitrogen, anchovy require an absorbed ration of 2.17 mgN. g dry wt^{-1}. day^{-1}, equivalent to 1.45% of their body N/day. This is greater than the

absorbed rations of Experiments 4, 7, 8, 9, 10, 11, 12 and 13.

DISCUSSION

Enzyme Activity

The data clearly indicate that there is an induction of enzyme activity at the onset of feeding. The lag in æ-amylase activity may be attributed to the fact that it was largely restricted to the pyloric caeca (Table 3); blind intestinal passages known to harbour large populations of bacteria (Seiderer et al 1987) and implicated in long term digestion of food (Peters and Kjelson 1975). This distribution of á-amylase activity supports the findings of Piavaux (1973) and Danulat (1986) for other teleosts and Seiderer *et al* (1987) for *E.capensis*, who found that carbohydrate digestion occurred mainly after the food had passed into the posterior section of the gut.

Laminarinase activity was also concentrated in the latter portion of the intestine. However, the similartiy between the exponential decline in enzyme activity and the faecal elimination rate, together with the marked posterior shift of activity with time (Table 3) could indicate that the bulk of this enzyme was of exogenous i.e. associated with the ingested prey, rather than endogenous origin. This would be in contrast to the results of

Seiderer *et al* (1987) who stated that E. capensis was capable of expoiting diatoms, whose major storage product is chrysolaminarin (Myklestad 1978).

Protease and chitinase activities had similar time courses (Fig. 1), but were concentrated in different sections of the alimentary canal. The concentration of protease activity in the oesophagus and caeca disagrees with the results of Torrissen (1974) for salmonids and Seiderer et al (1987) for *E. capensis*, who both found that proteases were concentrated in the intestine, with no evidence of proteolytic activity in the oesophagus or stomach. It is unlikely that much of the proteolytic activity in the anterior portions of the alimentary tract was associated with the zooplanton food since activity levels remained high in the oesophagus after the ingestion of prey was complete (Table 3).

The prominence of chitinase activity in the intestine and stomach and its virtual absence from the oesophagus is of interest. Seiderer *et al* (1987) found chitinase activity to be low and concentrated in the oesophagus of *E. capensis*. They stated that its primary function was to disrupt the exoskeleton to allow effective digestion of the prey by enzymes present in the stomach and intestine and was located in the oesophagus for this purpose. The present data do not support this, but rather indicate that the bulk of the enzyme originates in the stomach (Table 3).

TABLE 6: A comparison of the gastric evacuation and faecal elimination rates of juvenile and adult *B. tyrannus*, adult *E. mordax* and *E. capensis*.

SPECIES	SIZE mm	TEMP. °C.	PREY	EVACUATION/ ELIMINATION RATE	REFERENCE
B. TYRANNUS	27 - 32	15	*A. salina* nauplii	-0.28	Kjelson *et al* (1975)
	27 - 32	16	Copepods	-0.17	
	258	20	*Ditylum brightwelli*	-0.366 ± 0.046	Durbin and Durbin (1981)
E. MORDAX	± 120	16	*E. mordax* eggs	-0.76	Hunter and Kimbrell (1980)
	107 - 121	15	Trout pellets	-0.30	Hunter and Leong (1981)
				-0.44	
E. CAPENSIS	88 - 101	16	*A. salina*	-0.227 ± 0.055	Present Study
			A. salina & *P. crassirostris*	*-0.107*	
			A. salina & *C. finmarchicus*	*-0.058*	
			Paracalanus	-0.085	
			Cladocera	-0.119 ± 0.016	
			Chaetoceros	-0.025	

Danulat (1986) found that the major portion of chitinase activity in cod, *Gadus morhua*, fed upon fish and crustacean diets was restricted to the pyloric caeca. The pattern of chitinase activity in the alimentary tract during the time course suggests that some of the activity may be associated with the prey. The concentration of activity in the intestine at t = 0 hrs could be attributed to the remains of the last meal (Table 3) and the movement of the peak in activity from the stomach at t = 2.5 to the intestine at t = 24.75 (Table 3) could be due to the movement of the meal through the alimentary canal. Seiderer *et al* (1987) also indicated that some chitinase activity could arise from the food.

The absence of chitinase from various sections of the alimentary tract at all times except t = 2.5 (Table 3) is also surprising since chitinase activity was noted throughout the intestinal tract of *E. capensis* by Seiderer *et al* (1987) and Danulat (1986) detected chitinase activity in samples of stomach, pyloric caeca and stomach tissue from cod that had been starved for three weeks.

Faeces Elimination

There are few measurements of gastric evacuation or faecal elimination rates for clupeids (Table 6). Durbin and Durbin (1981) showed that there was good agreement between the predicted gastric evacuation and observed faecal elimination rates in

B. tyrannus. For comparative purposes it has been assumed that this result holds for the other species discussed.

The exponential model of faecal elimination or gastric evacuation was suitable for the data collected since the elimination rates declined exponentially after the end of feeding.

There was wide variation in the coefficient of the exponential decline in elimination rates. *A. salina* produced the most rapid (mean ± S.D. = -0.227 ± 0.055 hr^{-1}), the diatom *Chaetoceros* spp the slowest elimination rate (-0.025 hr^{-1}) and a variety of zooplankton diets a series of intermediate values (Table 4). This variation may be attributed to the different food types offered. Food quality is an important influence on the evacuation rate of a meal (Quigley and Meschan 1941; Pandian 1967; Kitchell and Windell 1968; Elliot 1972). Although the degree of chitinisation of the prey is apparently unimportant (Elliot 1972), the lipid content of the food is known to delay gastric evacuation in other vertebrates (Quigley and Meschan 1941; Elliot 1972). However, *E. mordax*, and presumably other clupeids, have a general facility to hydrolyse wax esters (Patton *et al* 1975) - the main storage products of zooplankton. Blaxter and Hunter (1982) suggested that the more easily digestible food types would be evacuated more rapidly. The data available for juvenile *B. tyrannus*, *E. mordax* and *E. capensis* support this hypothesis (Table 6).

The elimination coefficients for *E. capensis* agree well with those determined for juvenile *B. tyrannus* (Kjelson *et al* 1975) feeding on similar diets (Table 6). However the values for *E. capensis* are 1/2 - 1/10 those recorded for E.mordax (Table 6). This is surprising and of some significance since these species are biologically and ecologically similar, and Hunter and Kimbrell's value of -0.76 has been used to estimate the importance of egg cannabalism in *E. capensis* (Valdes *et al* 1987). It is possible that Hunter and Kimbrell's (1981) estimate of evacuation rate, although correct for the laboratory conditions under which it was determined, is of limited ecological value. The anchovy were fed a diet of pure anchovy eggs, which are extremely easily digested (Valdes *et al* 1987) and will thus be rapidly eliminated from the alimentary tract. It is, however, unlikely that anchovy in the field will feed solely upon their own eggs, especially if larger, more visible food is available (Chapters two and four). The presence of less digestible items, such as crustaceans and diatoms, in the diet would reduce the evacuation rate. It is obvious that further experimental work is required to determine the feeding rate and selective pressure of anchovy upon their own eggs and the exponential elimination coefficients of diets containing anchovy eggs and other planktons as they occur in the wild.

TABLE 7: Some examples of assimilation efficiencies of teleosts fed diets containing a variety of animal and vegetable matter.

SPECIES	FOOD	ASSIMILATION EFFICIENCIES % CARBON	NITROGEN	ENERGY	REFERENCE
Engraulis capensis	Zooplankton	77.88±7.22	87.38±4.28		This study
	Phytoplankton	50.57±0.69	83.21±1.80		
Brevoortia tyrannus	Zooplankton	91.43±0.35	93.99±0.74	87.67±1.67	Durbin and Durbin
	Phytoplankton	88.51±1.76	93.61±1.25	89.54±2.77	(1981)
Tilapia nilotica	*Nitzschia*	79			Moriarty and Moriarty
	Microcystis	70			(1973)
	Anabaena	75			
	Chlorella	49			
Haplochromis nigripinnis	*Microcystis*	71			
Holacanthus bermudensis	*Monostroma*		82 - 91	72 - 84	Menzel (1959)
	Enteromorpha				
Epinephelus guttatus	*Anchoa choerostoma*			96.10±0.40*	Menzel (1960)
	Sardinella anchovia			91.75+	
	Harengula callolepis			96.90±0.40@	
Megalops cyprinoides	*Metapenaeus monoceros*		96.80±2.00	91.50±2.70	Pandian (1967)
Ophiocephalus striatus	*M. monoceros*		97.10±1.30	90.60±1.60	Pandian (1967)
Fundulus heteroclitus	*Palaemonetes*		94.6	92.4	Weisberg and Lotrich
	Nereis		97.1	76.9	(1982)
	Uca pugnax		83.6	92.4	
	Amphipoda			87.2	Targett (1979)
Fundulus notatus (1972)	*Insecta*			90.0	Atmar and Stewart
Stizostedium vitreum vitreum	Emerald shiner			97.9	Kelso (1972)
	Perch			96.9	(Data suspect due to
	Crayfish			83.5	errors in conversion
	Amphipods			81.2	from mass to calories in Table 1.)
Lepomis machrochirus	Mealworms		94.30±0.67		Gerking (1955a)
Cyprinus carpio	Assorted invertebrates (mainly arthropods)			±89	Ivlev (1939)

* 19°C + 23°C @ 28°C

Absorption Efficiencies

E. capensis absorbed zooplankton C and N more efficiently than the phytoplankton counterparts (Table 5). The N absorption efficiencies for *E. capensis* are similar to or less than those reported for other fishes (Table 7). The zooplankton C absorption efficiency is somewhat lower than that recorded for the phytophagous *B. tyrannus* (Table 7). However, the present data are not corrected for the chitin content of the prey, which is known to reduce absorption efficiencies (Durbin and Durbin 1981; Weisberg and Lotrich 1982). The Cape anchovy is markedly less efficient than other fishes at utilising phytoplankton C (Table 7).

It has often been observed that absorption efficiencies vary with food type and quality (Pandian 1967; Beamish 1972; Durbin and Durbin 1981). The higher absorption efficiencies for zooplankton relative to phytoplankton indicate that the former are more suitable food for the anchovy and provides physiological evidence to support the hypothesis that *E. capensis* is primarily carnivorous (Chapters two and four).

Ration size and feeding time had no effect upon the absorption efficiencies (Table 5). This is in general agreement with the majority of observations in the literature (e.g. Pandian 1967; Beamish 1972; Kelso 1972), although Elliot (1972), Elliot and Persson (1978) and Durbin and Durbin (1981) found that efficiencies

decreased with increasing ration size.

The absorption efficiencies of *E. capensis* usually remained approximately constant throughout an experiment (Fig. 3a) and there was no relationship between the faecal elimination rate and N absorption efficiency (Fig. 4). This contrasts with the findings of Durbin and Durbin (1981), who observed that efficiencies rose from initial low values to a peak during feeding and thereafter were related to the faecal elimination rate. This pattern was observed for Exps. 5, 10 and 11 in the present study (Fig. 3a and 3b). Durbin and Durbin (1981) reasoned that these changes were due to either a lag in enzyme secretion, or the addition of material secreted by the gut to the faecal pellets. However, the data presented here indicate that enzyme induction is rapid, generally peaking by the end of feeding activity (Fig. 1) and is therefore unlikely to account for the initial low values during Exp. 11 (Fig. 3). During Exps. 5 and 10 the mucous sheath was more prominent and mucous strands were associated with the faeces during the latter stages of the experiments. The elimination of material not associated with the ingested ration would cause a reduction in the absorption efficiencies as described by Durbin and Durbin (1981).

Nitrogen Excretion

Ammonia is the major excretory product of most teleosts (Smith 1929; McCarthy and Whitledge 1972; Watts and Watts 1974; Brett and Zala 1975; Savitz et al 1977; Durbin and Durbin 1981). The present data do not allow us to accertain the composition of the N excreted by E. capensis. Instead, total organic N excretion has been estimated from the data of Durbin and Durbin (1981).

N excretion by *E.capensis* followed a similar pattern to that reported in the literature for a variety of other fishes (Brett and Zala 1975: Elliott 1976: Savitz et al 1977; Weisberg and Lotrich 1982; Durbin and Durbin 1981) and was dependent upon the size of ration, feeding rate, duration of feeding and the level of activity of the fish. However, the cycle observed was faster than that noted for most species (Brett and Zala 1975; Elliot 1976; Savitz *et al* 1977), being similar to that reported for the menhaden (Durbin and Durbin 1981). Nitrogen excretion only lagged 2 - 4 hours behind the ingestion of the ration with only a mean of 1.83 ± 0.74 hours elapsing between the mid-point of feeding and 50% of the N being excreted; 90% of the N was excreted within a mean of 3.85 ± 1.77 hours of the end of feeding. The time taken to return to routine levels was apparently dependent upon the activity status of the fish. This was clearly illustrated during Exp. 14 when the fish maintained a high level of activity after the feeding period and the N excretion rate remained

TABLE 8: A comparison of the routine/ basal total N excretion rates of clupeids.

SPECIES	EXCRETION RATE µg N/ g dry wt./ day	REFERENCE
Engraulis capensis	34.93 ± 4.32	This study
Engraulis mordax	11.38	McCarthy and Whitledge (1972)
Engraulis ringens	19.02 ± 7.89	McCarthy and Whitledge (1972)
Brevoortia tyrannus	10.72 ± 3.65	Durbin and Durbin (1981)

elevated above routine rates for an unusually long period of time (Table 4).

The lag between ingestion and N excretion appeared to be slightly shorter in the menhaden that the Cape anchovy (c.f. time between the midpoint in feeding and 50% of N excreted in menhaden 1.4 ± 0.5 hours and 90% of N excreted 2.4 ± 1.6 hours after end of feeding). This may be due to the menhaden being fed similar ration sizes over a longer period of time (6 - 8 hours compared to 2 - 5.5 hours for the present experiments). There is a lag between the peak NH4 and urea rates after the start of feeding, indicating that the NH4 : Urea, and hence the DON : NH4 ratios are not constant. McCarthy and Whitledge (1972) also observed that the urea : NH4 ratio's varied in E. mordax excretion, stating that the effect of feeding was more rapidly evident in the NH4 release rates and appeared more slowly and to a lesser extent in the urea rates.

The routine excretion rates of E. capensis are 2 - 3 times greater than those recorded for other clupeids (Table 8). The differences between the three closely related anchovy species may be due to differences in experimental conditions, the level of activity and degree of stress suffered by the fish. We are confident of the rates for *E. capensis*, since the fish were apparently unstressed since the fish exhibited natural behaviour patterns (schooling and feeding) under our experimental conditions. The smaller,

more active anchovy would be expected to have a higher excretion rate that the menhaden.

A constant proportion of ingested and absorbed rations were excreted by the anchovy (41.5% and 47.8% respectively). Similar relationships have been determined for other species (Gerking 1971; Savitz et al 1977; Durbin and Durbin 1981; Weisberg and Lotrich 1982). *E. capensis* retains approximately the same proportion of a ration as the largemouth bass, *Micropterus salmoides*, (±60%; Savitz *et al* 1977), but more than that of *B.tyrannus* (38.5% of the ingested and 34.5% of the absorbed ration; Durbin and Durbin 1981). The Cape anchovy requires a considerably larger maintenance ration of N (pR_N 2.17 mgN. g dry wt^{-1}. day^{-1}) than the phytophagous *B. tyrannus* (pR_N = 0.70 mgN. g dry wt^{-1}.~day^{-1}) or the bluegill sunfish, *Lepomis machrochirus* (0.94 mgN. g dry wt^{-1}. day^{-1} and 0.75 mgN. g dry wt^{-1}. day^{-1}; Gerking 1955a; b respectively). This is in agreement with the general finding that *E. capensis* has a higher metabolic rate than *B. tyrannus*. The difference between the requirements of the anchovy and sunfish may be largely attributable to differences in the level of activity of the two species during the experiments. *L. machrochirus* inhabits stagnant areas of creeks and ponds and is less active than a fish such as the anchovy. The maintenance requirement calculated for *E. capensis* incorporated a good deal of spontaneous activity (This study; Chapter five) which was not included in the calculation of the N maintenance ration of the

bluegill sunfish.

The relationships between the ration size and excretion and between growth effeciency and ration size are important components required for the construction of nitrogen budgets for *E. capensis*. The absorption efficiency data indicate that *E. capensis* is capable of efficiently processing its prey, either under a continuous feeding regime or in short periods of intense feeding activity. As such this species is physiologically well equipped to utilise a patchy zooplankton distibution, as is typical of the Southern Benguela.

CONCLUSIONS

1. There is a rapid induction of enzyme activity after the onset of feeding.

2. A constant proportion of the faeces is eliminated per unit time; the rate being dependent upon food type.

3. In terms of C and N, *E. capensis* utilises zooplankton more efficiently that phytoplankton.

4. The rate of excretion of N from a meal, which only lags ingestion by 2 - 4 hours, is dependent upon ration size, feeding rate and time and the activity status of the fish.

5. A constant proportion of the N of the ingested or absorbed ration is excreted.

CHAPTER SEVEN

Laboratory derived carbon and nitrogen budgets for the omnivorous planktivore *Engraulis capensis* Gilchrist.

To be submitted to the Journal of Experimental Marine Biology and Ecology.

INTRODUCTION

The consideration of bioenergetics can provide valuable information regarding the effects of biotic and abiotic factors on the growth of an organism. Considerable field and laboratory data are available concerning the trophic ecology and physiological and behavioural responses of the Cape anchovy, *Engraulis capensis*, to a variety of plankton conditions (Chapters two, four, five and six). These data may be utilised to construct carbon and nitrogen budgets to quantify the effects of changes in the fishes trophic environment upon the total (somatic and reproductive) growth of the fish.

Previous work demonstrated that prey size was the single most important factor affecting the feeding behaviour, and food consumption and respiration rates of *E. capensis* (Chapters four and five). The budget models presented were developed to analyse the effect of prey size upon the growth of *E. capensis* under the foraging regime and plankton densities observed in the Benguela region (Andrews and Hutchings 1980; Shannon and Field 1984; Shannon and Pillar 1986 and references therein; Pillar 1986; Mitchell-Innes et al in prep.; Brown and Hutchings 1987; James 1987; Hutchings 1988 and Verheye and Hutchings 1988). The budgets are based upon experimental data collected from age 0 anchovy of mean length 100.4mm, and mean wet and dry weights of 7.28g and 2.33g respectively. The mean water temperature was 16.2 °C.

TABLE 1. Summary of the symbols.

Gc / G_N	Total daily growth (mgC.gdry $wt^{-1}.day^{-1}$/mg N.g dry $wt^{-1}.day^{-1}$)
Rc / R_N	Total daily food consumption (mgC.gdry $wt^{-1}.day^{-1}$/mg N.g dry $wt^{-1}.day^{-1}$)
Tc	Total daily oxygen consumption (mgC.g dry $wt^{-1}.day^{-1}$)
Tr	Routine respiration rate (mgO_2.gwet $wt^{-1}.hr^{-1}$)
Tf	Respiration rate during filterfeeding (mgO_2.g wet wt^{-1}. hr^{-1})
Tp	Respiration rate during particulate feeding (mgO_2.g wet wt^{-1}. hr^{-1})
Trc	Total daily routine oxygen consumption (mgC.gdry $wt^{-1}.day^{-1}$)
Tfc	Total daily oxygen consumption during filterfeeding (mgC.gdry $wt^{-1}.day^{-1}$)
Tpc	Total daily oxygen consumption during particulate feeding (mgC.gdry $wt^{-1}.day^{-1}$)
Ec / E_N	Total daily nitrogen excretion (mgC.gdry $wt^{-1}.day^{-1}$/mg N.g dry $wt^{-1}.day^{-1}$)
Fc / F_N	Total daily losses through defaecation (mgC.gdry $wt^{-1}.day^{-1}$/mg N.g dry $wt^{-1}.day^{-1}$)
v	Volume searched by a fish during feeding (l. $fish^{-1}.hr^{-1}$)
A	Efficiency of searching (dimensionless)
F	Clearance rate (l. $fish^{-1}.min^{-1}$)
p	Absorption efficiency (dimensionless)
s	Swimming speed ($cm.s^{-1}$)
P	Prey size (mm)
C/N	Food concentration (mg C l^{-1}/mg N.l^{-1})
h	Foraging time ($hrs.day^{-1}$)
K_{1C}/K_{1N}	Gross growth efficiency = Gc/Rc and G_N/R_N (dimensionless)
K_{2C}/K_{2N}	Net growth efficiency = Gc/pRc and G_N/pR_N (dimensionless)

Carbon and nitrogen were chosen as the currencies for the budgets since they are key elements required for growth and because they provide an easy reference standard to compare and utilise field and laboratory data.

CARBON BUDGETS

The budgets are based upon the general growth equation:

$G_C = R_C - T_C - E_C - F_C$ (Durbin and Durbin 1983) 1

The symbols used in the development of the budgets are summarised in Table 1.

Daily Carbon Intake

Ingested Ration R_c

The amount of food ingested by the anchovy depends upon the volume searched (v), the efficiency with which the food is removed from that volume (A), the plankton concentration (C) and the foraging time (h).

$Rc = v \times A \times C \times h$ $mgC.fish^{-1}.day^{-1}$ 2

(Durbin and Durbin 1983).

However, although v and A are relatively easy to define for both filter and particulate feeding (Werner and Hall 1974; Eggers 1977; O'Brien et al 1976; Ware 1978; Durbin and Durbin 1975; Chapter four), they are very difficult to measure practically.

Durbin and Durbin (1975) defined the volume searched for the filterfeeding *Brevoortia tyrannus* as the product of the mouth area and the swimming speed of the fish, while James (Chapter four) assumes that the v is equivalent to the maximum observed filtration rate. Both these approaches provide fixed values of the volume searched, against which all observed filtration rates can be compared to estimate efficiency. Neither approach can account for dynamic behaviour changes which might occur when the fish fed on different food types or as food concentrations changed, such as the duration and rate of mouth opening. The problem of measuring the volume v and A during particulate feeding is even more intractable. The volume searched by a particulate feeder is primarily dependent upon the visual field of the predator, which is affected by a wide variety of biotic and abiotic factors including the visual acuity, swimming speed, reactive distance and degree of fullness of the predator, prey size and swimming speed, the contrast between the prey and surrounding environment, the ambient light level and attenuation coefficient of the environment (Werner and Hall 1974; O'Brien et al 1976; Eggers 1977; Ware 1978). Most of these factors are difficult or impossible to measure, especially when it is considered that most are dynamic processes which would require continuous monitoring to provide the necessary data to determine the search volume of a planktivorous predator. In Chapter four an attempt to quantify the visual range and reactive distance of *Engraulis capensis* is reported, but I was unable to relate these data to

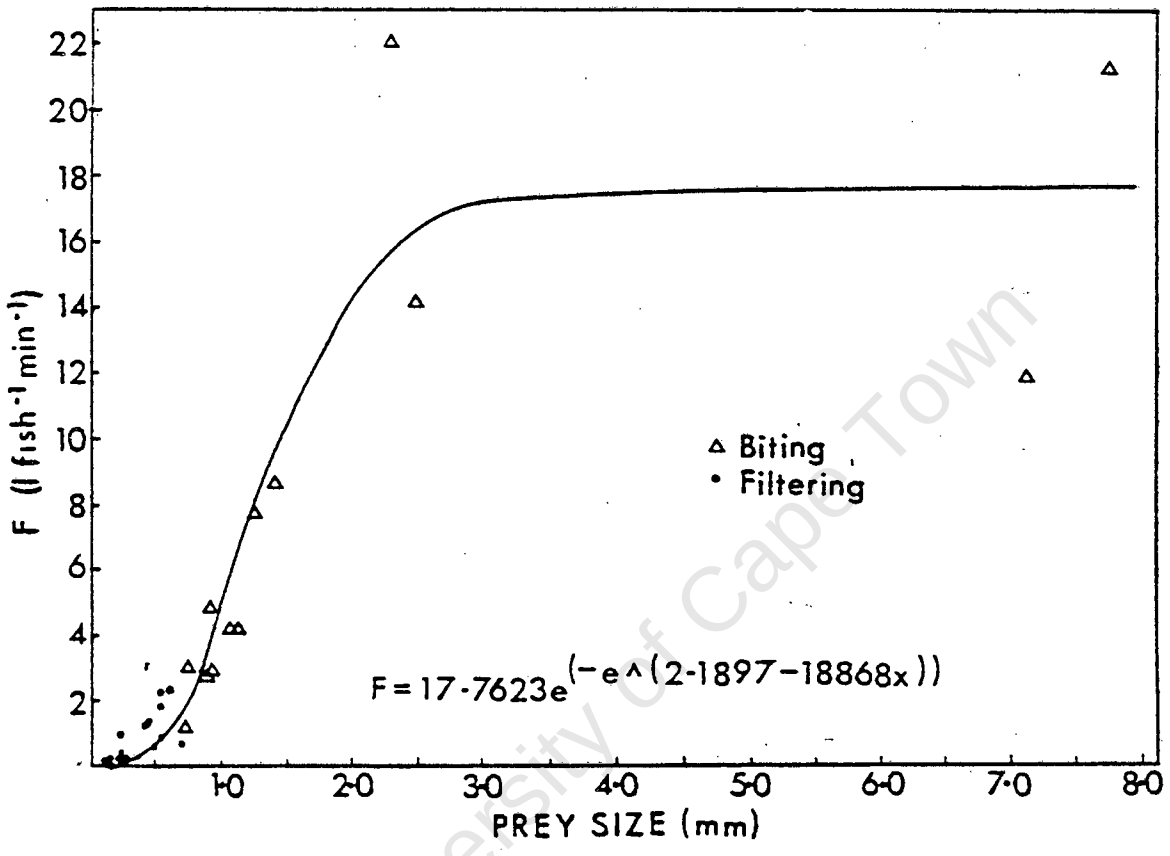


FIGURE ONE. : Clearance rates (F l/fish/min) of Cape anchovy as a function of prey size (mm). From Chapter Two.

the measured clearance rates.

Estimating values of the volume searched and efficiency for use in the models may be avoided by utilising the observed clearance rates (F l.fish^{-1}.min^{-1}) of the fish feeding upon a variety of plankton foods (Durbin and Durbin 1975; Chapter four). These empirical data are the product of the two variables and account for the dynamic processes affecting them.

$$F = v \times A \qquad 3$$

To convert to l fish^{-1}hr^{-1} multiply F by 60. Therefore, equation 2 may be rewritten

$$Rc = (60F)Ch \qquad 4$$

However, in Chapter four, it was found that the clearance rate (F) was dependent upon prey size (P), (Fig. 1):

$$F = 17.7623e^{(-e^{(2.1897 - 1.8868P)})}\ \text{l.fish}^{-1}.\text{min}^{-1}. \qquad 5$$

Combining equations 4 and 5 allows us to express carbon gain in terms of prey size (P), plankton concentration (C) and foraging time (h):

$$R_c = (60 \times 17.7623e^{(-e^{(2.1897 - 1.8868\ P)})})\ Ch$$

$$\text{mgC.fish}^{-1}.\text{day}^{-1}$$

$$= 1065.7e^{(-e^{(2.1897 - 1.8868P)})}\ Ch \qquad 6$$

$$\text{mgC.fish}^{-1}.\text{day}^{-1}$$

The mean dry weight of the experimental fish was 2.33g.

$$Rc = 457.4e^{(-e^{(2.1897 - 1.8868\ P)})}\ Ch \qquad 7$$

$$\text{mgC.g dry wt}^{-1}.\text{day}^{-1}$$

TABLE 2. Absorption efficiencies for Engraulis capensis fed phytoplankton and zooplankton. From Chapter six.

	ABSORPTION EFFICIENCY	
ELEMENT	PHYTOPLANKTON	ZOOPLANKTON
CARBON	50.57 ± 0.69	77.88 ± 7.22
NITROGEN	83.21 ± 1.80	87.38 ± 4.28

Absorbed Ration pR_C

If the faecal losses (F_C) are subtracted from the ingested ration (R_C), then a measure of the absorbed ration (pR_C) is obtained:

$$p = \frac{R_C - F_C}{R_C} \qquad 8$$

James (Chapter six) determined mean carbon and nitrogen assimilation efficiencies of *E. capensis* for zooplankton and phytoplankton diets (Table 2). Equation 1 may thus be rewritten as:

$$G_C = pR_C - T_C - E_C \quad \text{mgC.g dry wt}^{-1}\text{.day}^{-1} \qquad 9$$

where pRc is given by:

Phytoplankton

$$pR_C = 0.5057R_C \quad \text{mgC.g dry wt}^{-1}\text{.day}^{-1}$$

$$= 231.3e^{(-e^{(2.1897 - 1.8868P)})}Ch \qquad 10$$

$$\text{mgC.g dry wt}^{-1}\text{.day}^{-1}$$

Zooplankton

$$pR_C = 0.7788R_C \quad \text{mgC.g dry wt}^{-1}\text{.day}^{-1}$$

$$= 356.2e^{(-e^{(2.1897 - 1.8868P)})}Ch \qquad 11$$

$$\text{mgC.g dry wt}^{-1}\text{.day}^{-1}$$

Daily Carbon Losses

1) Respiration T_c

Respiration represents the major source of carbon expenditure during routine (non feeding) and feeding activity.

Daily Cost of Routine Respiration T_{rc}

The mean measured routine (nonfeeding) respiration rate (T_r) and swimming speeds were 0.111 mgO_2.g wet wt^{-1}. hr^{-1} and 16.09 $cm.s^{-1}$ respectively. Converting to dry weight,

T_r = 0.347 mgO_2.g dry $wt^{-1}.hr^{-1}$ 12

James (Chapter four) determined that the mean respiratory quotient (RQ) of *E. capensis* was 0.915 +/- 0.183. The respiration rate may be converted from O_2 to C currency using the relationship quoted in Parsons et al (1984):

mgC utilised = mgO_2 consumed x 12/32 x RQ

Therefore:

T_r = 12/32 x 0.915 x 0.347 mgC.g dry $wt^{-1}.hr^{-1}$

= 0.12 mgC.g dry $wt^{-1}.hr^{-1}$ 13

The daily cost of routine respiration is therefore

T_{rc} = 0.12 (24 - h) mgC.g dry $wt^{-1}.day^{-1}$ 14

Daily Costs of Respiration During Feeding T_{fc} and T_{rc}

Swimming speed was the primary influence on respiration rate during feeding, accounting for 93.9% and 78.5% of its variability during filter and particulate feeding respectively (Chapter

five). Other factors which could influence the respiration rate during feeding are excitement and the specific dynamic affect (SDA) of the food (Beamish 1972, 1974; Durbin et al 1981). The data available indicate that the fish were least excitable while feeding, although the level of excitement was greater during particulte than during filter feeding (Chapter five). The digestion and absorption of the ration occurred largely within the period of elevated activity during this study and that of Durbin et al (1981) and therefore the SDA of the food was not quantified. In any event, the effect of a small fixed metabolic cost such as the SDA would be overshadowed by variations in swimming speed during the feeding and post feeding periods (Durbin and Durbin 1981; Chapter five). For the purposes of the carbon budgets, it has been assumed that the metabolic cost of the SDA is included in the respiration rates during the period of elevated activity.

Respiration rates, and hence carbon losses, during feeding are dependent upon feeding mode, which is in turn, influenced by prey size (Chapter five). The respiration rate increases significantly faster per unit increase in swimming speed during filter than during particulate feeding due to the loss of streamlining caused by the gaping mouth and flared opercula (Chapter five). Observations and experimental data indicate that there is a switch from filterfeeding to particulate feeding at prey sizes of approximately 0.70mm. Therefore the following rule may be applied to carbon losses through respiration during feeding:

for prey sizes below 0.7mm the filterfeeding relationship between T and s will apply:

$\log_{10}T_f = 0.042s - 1.669$ $mgO_2.g$ wet $wt^{-1}.hr^{-1}$. 15

(Table 4, Chapter five). For prey sizes above 0.7mm the particulate feeding relationship between T and s will apply:

$\log_{10}T_p = 0.025s - 1.226$ $mgO_2.g$ wet $wt^{-1}.hr^{-1}$ 16

(Table 4, Chapter five). Equations 15 and 16 may be rewritten as:

$T_f = 10^{0.042s - 1.669}$ $mgO_2.g$ wet $wt^{-1}.hr^{-1}$ 17

and

$T_p = 10^{0.025s - 1.226}$ mgO_2. g wet$wt^{-1}.hr^{-1}$ 18

Converting to dry weight and expressing respiration costs in terms of carbon:

Filterfeeding

$T_f = 12/32 \times 0.915 \times 3.13(10^{0.042s - 1.669})$

$mgO_2.g$ dry $wt^{-1}.hr^{-1}$

$= 1.07(10^{0.042s - 1.669})$ mgC.g dry $wt^{-1}.hr^{-1}$ 19

Particulate feeding:

$T_p = 12/32 \times 0.915 \times 3.13(10^{0.025s - 1.226})$

$mgO_2.g$ dry $wt^{-1}.hr^{-1}$

$= 1.07(10^{0.025s - 1.226})$ mgC.g dry $wt^{-1}.hr^{-1}$ 20

Total respiration during feeding per day is therefore calculated by multiplying by the foraging time per day (h hrs.day^{-1})

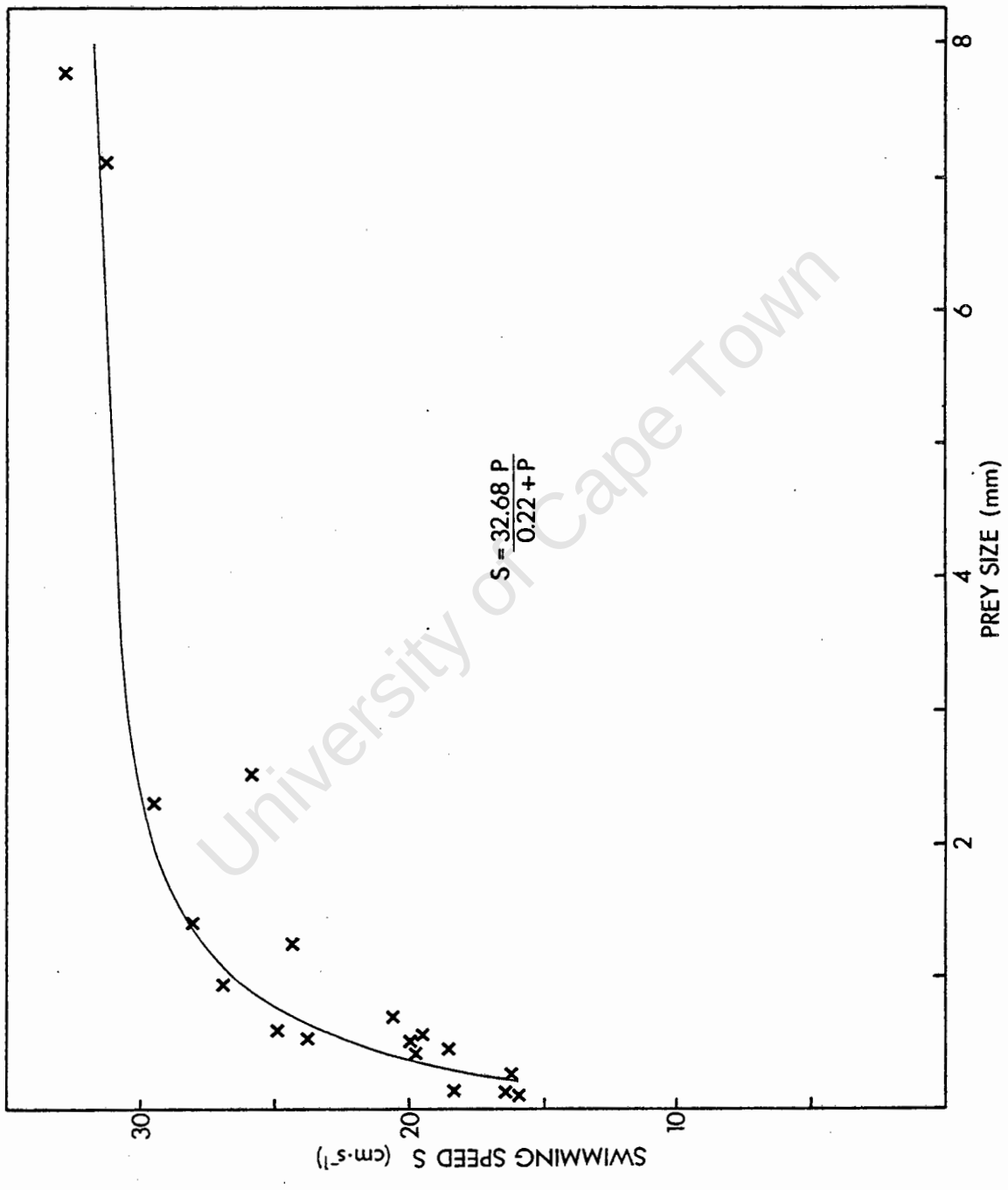
Filter feeding:

$T_{fC} = 1.07h(10^{0.042s - 1.669})$ mgC.g dry $wt^{-1}.day^{-1}$ 21

Particulate feeding:

$T_{pC} = 1.07h(10^{0.025s - 1.226})$ mgC.g dry $wt^{-1}.day^{-1}$ 22

FIGURE TWO. Swimming speed of feeding anchovy as a function of prey size.



Data from Chapters four and five indicate that there is a hyperbolic relationship between the mean swimming speed during feeding (s cm.s^{-1}) and prey size (P mm, Fig. 2):

$$s = \frac{32.68P}{0.22 + P} \qquad 23$$

Equation 23 may be substituted into 23 and 24 to give T in terms of P.

$$T_{fC} = 1.07h(10^{0.042(32.68P/0.22+P)} - 1.669)$$

mgC.g dry wt^{-1}.day^{-1}

$$= 1.07h(10^{(1.370P/0.22+P)} - 1.669) \qquad 24$$

mgC.g dry wt^{-1}.day^{-1}

and

$$T_{PC} = 1.07h(10^{0.025(32.68P/0.22+P)} - 1.226)$$

mgC.g dry wt^{-1}day^{-1}

$$= 1.07h(10^{(0.817P/0.22+P)} - 1.226) \qquad 25$$

mgC.g dry wt^{-1}.day^{-1}

Total daily carbon losses through respiration (T_c) are calculated by combining the routine and feeding respiration costs (equations 14 and 24 or 25).

$$T_{rC} + T_{fC} = T_C$$

$$T_{rC} + T_{PC} = T_C$$

Filterfeeding:

$$T_C = 0.12(24 - h) + 1.07h(10^{(1.37P/0.22+P)} - 1.669)$$

mgC.g dry wt^{-1}.day^{-1}

$$= 2.88 - 0.12h + 1.07h\,(10^{1.37P/0.22+P)} - 1.669)$$

mgC.g dry wt^{-1}.day^{-1}

$$= h[1.07(10^{(1.37P/0.22+P)} - 1.669) - 0.12] + 2.88 \quad 26$$

mgC.g dry wt^{-1}.day^{-1}

Particulate Feeding:

$$T_C = 0.12(24 - h) + 1.07h\,(10^{(0.817P/0.22+P)} - 1.226)$$

mgC.g dry wt^{-1}.day^{-1}

$$= h[1.07(10^{(0.817P/0.22+P)} - 1.226) - 0.12] + 2.88 \quad 27$$

mgC.g dry wt^{-1}.day^{-1}

Hence carbon losses have through respiration been expressed in terms of P and h.

2) Total Daily Excretion E_C

Following the work of Durbin and Durbin (1981) 30.4% of the nitrogen excretion has been assumed to be organic. McCarthy and Whitledge (1972) found that the bulk of the identified organic excretion of Engraulis mordax was composed of urea and for the purposes of this model all organic excretion will be considered to be urea. The C:N ratio by molecular weight of urea (CH_4ON_2) is 0.5C : 1N, i.e. 0.5 atoms C are lost for every 1 atom of N excreted. Therefore, 1g of organic N excretion is equivalent to 12/14 x 0.5 gC and 0.304(12/14 x 0.5) gC = 0.13 gC is lost for every 1g of total N excreted.

Total daily losses through nitrogen excretion are the sum of endogenous (basal) and exogenous (due to feeding) excretion. Chapter six showed that the Cape anchovy excretes a constant proportion of the ingested ration and that total daily N excretion

(E_N) was linearly related to the ingested ration (R_N):

$E_N = 1.112 + 0.415\ R_N$ mgN.g dry wt^{-1}.day^{-1} 28

In terms of carbon:

$E_C = 0.13(1.112) + 0.13(0.415\ R_N)$ mgC.g dry wt^{-1}.day^{-1}

$= 0.145 + 0.054\ R_N$ mgC.g dry wt^{-1}.day^{-1} 29

Using the C:N ratios of the different food types:

phytoplankton C:N = 5.32:1 30

zooplankton C:N = 4.66:1 31

found in Chapter six, and substituting the appropriate C:N ratios into equation 29, carbon losses through nitrogen excretion may be expressed entirely in terms of carbon:

Phytoplankton

$E_C = 0.145 + 0.19(0.054\ R_N)$ mgC.g dry wt^{-1}.day^{-1}

$= 0.145 + 0.010\ R_C$ mgC.g dry wt^{-1}.day^{-1} 32

Zooplankton

$E_C = 0.145 + 0.21(0.054\ R_N)$ mgC.g dry wt^{-1}.day^{-1}

$= 0.145 + 0.011$ Rc mgC.g dry wt^{-1}.day^{-1} 33

Equation 7 may be substituted into equations 32 and 33 so that carbon loss through excretion (E_C) is expressed in terms of the same three variables as R_C (P, C and h):

Phytoplankton

$E_C = 0.145 + 0.01(457.4e^{(-*^{(2.1897 - 1.8868P)})}$ Ch

mgC.g dry wt^{-1}.day^{-1}

$= 0.145 + 4.574e^{(-*^{(2.1897 - 1.8868P)})}$ Ch 34

mgC.g dry wt^{-1}day^{-1}

TABLE 3.Summary of the carbon budget equations.

CARBON BUDGETS mg C g dry wt^{-1} day^{-1}			
ENTITY	PHYTOPLANKTON	MICROZOOPLANKTON	MESOZOOPLANKTON
Rc		$457.4\, e^{(-b^{(2.1897 - 1.8868P)})} Ch$	
pRc	$231.3e^{(-b^{(2.1897-1.8868P)})}Ch$	$356.2e^{(-b^{(2.1897-1.8868P)})}Ch$	
Tc	$b \quad h[1.07(10^{(1.37P/0.22+P)-1.669}) - 0.12] + 2.88$		$h[1.07(10^{(0.817P/0.22+P)-1.226}) - 0.12] + 2.88$
Ec	$0.145+4.57e^{(-b^{(2.1897-1.8868P)})}Ch$	$0.145+5.03e^{(-b^{(2.1897-1.8868P)})}Ch$	
Gc	pRc - Tc - Ec		
K1c	Gc/Rc		
K2c	Gc/pRc		

Zooplankton

$$E_C = 0.145 + 0.011\ (457.4e^{(-*^{(2.1897 - 1.8868P)})})\ Ch$$

mgC.g dry wt^{-1}.day^{-1}

$$= 0.145 + 5.03e^{(-*^{(2.1897 - 1.8868P)})}\ Ch \qquad 35$$

mgC.g dry wt^{-1}.day^{-1}

Growth G_C

The equations summarised in Table 3 may be substituted into equation 9 to provide estimates of daily growth of *E. capensis* feeding on a variety of diets as a function of P, C and h; data that are readily available from laboratory and field studies.

The gross and net growth efficiencies (K_{1C} and K_{2C} respectively) may be calculated from the following expressions (Durbin and Durbin 1983):

$$K_{1C} = G_C/R_C \qquad 36$$

$$K_{2C} = G_C/pR_C \qquad 37$$

NITROGEN BUDGETS

The nitrogen budgets may be expressed in the same three components as the carbon budgets: prey size (P), plankton concentration (C or N) and foraging time (h). The nitrogen budgets are based upon the general equation:

$$G_N = R_N - E_N - F_N \quad \text{mgN.g dry wt}^{-1}\text{.day}^{-1} \qquad 38$$

which, like the carbon budget may be simplified to:

$G_N = pR_N - E_N$ mgN.g dry wt^{-1}.day^{-1} 39

Daily Nitrogen Intake

Ingested Ration R_N

Equation 7 may be rewritten in terms of nitrogen:

$R_N = 457.4e^{(-e^{(2.1897 - 1.8868P)})}$ Nh 40

mgN.g dry wt^{-1}.day^{-1}

The absorbed ration may be obtained by utilising the appropriate values from Table 2:

Phytoplankton

$pR_N = 0.8321R_N$

$= 380.6e^{(-e^{(2.1897 - 1.8868P)})}$ Nh 41

mgN.g dry wt^{-1}.day^{-1}

Zooplankton

$pR_N = 0.8738R_N$

$= 399.7e^{(-e^{(2.1897 - 1.8868P)})}$ Nh 42

mgN.g dry wt^{-1}.day^{-1}

Daily Nitrogen Losses

Excretion E_N

Equation 28 describes the relation between total daily nitrogen excretion and the ingested ration. Substituting equation 40 into equation 28:

$E_N = 1.112 + 0.415(457.4e^{(-*^{(2.1897 - 1.8868P)})} Nh)$

mgN.g dry wt^{-1}.day^{-1}

$= 1.112 + 189.8e^{(-*^{(2.1897 - 1.8868P)})} Nh$ 43

mgN.g dry wt^{-1}.day^{-1}

In order to standardise the currency of the input information for both the budgets, the nitrogen budget may be expressed in terms of carbon content of the plankton by utilising the appropriate C:N ratios (Expressions 30 and 31). Equations 40 - 43 then become respectively:

Phytoplankton

$R_N = 86.0e^{(-*^{(2.1897 - 1.8868P)})} Ch$ 44

mgN.g dry wt^{-1}.day^{-1}

$pR_N = 71.5e^{(-*^{(2.1897 - 1.8868P)})} Ch$ 45

mgN.g dry wt^{-1}.day^{-1}

$E_N = 1.112 + 35.7e^{(-*^{(2.1897 - 1.8868P)})} Ch$ 46

mgN.g dry wt^{-1}.day^{-1}

TABLE 4: Summary of the nitrogen budget equations

NITROGEN BUDGETS mg N g dry wt^{-1} day^{-1}

	PHYTOPLANKTON	ZOOPLANKTON
A) NITROGEN AS THE INPUT CURRENCY		
R_N	$457.4e^{(-*^{(2.1897-1.8868P)})}$ Nh	
pR_N	$380.6e^{(-*^{(2.1897-1.8868P)})}$ Nh	$399.7e^{(-*^{(2.1897-1.8868P)}}$Nh
E_N	$1.112+189.8e^{(-*^{(2.1897-1.8868P)}}$Nh	
B) CARBON AS THE INPUT CURRENCY		
R_N	$86.0e^{(-*^{(2.1897-1.8868P)})}$Ch	$98.2e^{(-*^{(2.1897-1.8868P)})}$Ch
pR_N	$71.5e^{(-*^{(2.1897-1.8868P)})}$Ch	$85.8e^{(-*^{(2.1897-1.8868P)})}$Ch
E_N	$1.112+35.7e^{(-*^{(2.1897-1.8868P)})}$Ch	$1.112+40.7e^{(-*^{(2.1897-1.8868P)})}$Ch
G_N	$pR_N - E_N$	
$K1_N$	G_N / R_N	
K_{2N}	G_N / pR_N	

Zooplankton

$R_N = 98.2e^{(-e^{(2.1897 - 1.8868P)})}$ Ch 47

mgN.g dry wt^{-1}.day^{-1}

$pR_N = 85.8e^{(-e^{(2.1897 - 1.8868P)})}$ Ch 48

mgN.g dry wt^{-1}.day^{-1}

$E_N = 1.112 + 40.7e^{(-e^{(2.1897 - 1.8868P)})}$ Ch 49

mgN.g dry wt^{-1}.day^{-1}

The equations summarised in Table 4 may be substituted into equation 39 to provide estimates of daily growth in nitrogen by *E. capensis* as a function of the same three variables as the carbon budgets; prey size (P), plankton concentration (C) and foraging time (h). Similarly to the carbon budgets, the gross and net growth efficiencies in terms of nitrogen are given by:

$K_{1N} = G_N/R_N$ 50

$K_{2N} = G_N/pR_N$ 51

RESULTS

The carbon and nitrogen budget models developed describe the interactions between the three variables; prey size (P mm), plankton concentration (C mgC. l^{-1}) and foraging time (h hrs. day^{-1}) and their effects upon the potential intake, expenditure, growth and growth efficiencies of *E. capensis* in carbon and nitrogen.

In the following examples used to illustrate the carbon and

TABLE 5 RANGES OF VARIABLES EMPLOYED TO GENERATE MODEL OUTPUTS

VARIABLE	MODEL OUTPUT: PHYTOPLANKTON		MICROZOOPLANKTON		MESOZOOPLANKTON	
	RANGE	STANDARD	RANGE		RANGE	
PREY SIZE P mm	0-0.4	0.25	0-0.7	0.5	0.7-3.0	2.0
PLANKTON CONCENTRATION C mg Cl^{-1}	0-1.0	0.5	0-0.5	0.1	0-0.1	0.05
FORAGING TIME h hrs.day^{-1}	0-24	12	0-24	12	0-8	4

nitrogen models, the three variables (P, C and h) were allocated different value ranges, depending upon food type (summarised in Table 5). The ranges were chosen to reflect the trophic conditions under which the anchovy operate in the Benguela system.

Phytoplankton

Diatoms form the main phytoplankton component in the diet of *E. capensis* (Chapter two). The upper limit of the prey size was set at 0.4mm in order to include the large solitary diatom genera, *Coscinodiscus*, which can form dense blooms in the St Helena Bay region during autumn (De Jager 1957; Mitchell-Innes pers. comm.), at which time it is grazed by the anchovy (James 1987). A fixed value of 0.25mm was assumed, since the observed clearance rate of *Chaetoceros* chains 0.11mm long was roughly equivalent to the clearance rate observed for the rotifer *Brachionus plicatilis* 0.256 mm long (Chapter four). The disparity between the prey sizes and clearance rates was due to the presence of long setae which increased the apparent size of the diatom cells (Chapter four). As *Chaetoceros* is one of the dominant diatom genera in the Benguela region, the apparent particle size rather than the real size was employed for the budget.

The phytoplankton concentration range (C = 0 - 1.0 mgC. l^{-1}) reflects the range observed in the Benguela region (Andrews and Hutchings 1980; Shannon and Field 1984; Shannon and Pillar 1986,

and references therein; Mitchell- Innes et al in prep; Mitchell-Innes pers. comm.; Brown and Hutchings 1987). The fixed value of 0.5mgC. l^{-1} approximates the phytoplankton density of a developed bloom in St Helena Bay (Pitcher 1986).

Foraging time was varied between 0 - 24 hours. day^{-1} on the assumption that if no particulate feeding occurred, the fish would filter feed at a low level throughout the 24 hours (Chapter two). The fixed value of 12 hours. day^{-1} was taken from James (Chapter two) who found that filter feeding generally occurred during the day.

Microzooplankton

For the purposes of this study, microzooplankton has been defined as all zooplankters that would elicit a filtering response from the anchovy - i.e. any particle smaller than 0.7mm (Chapter four). The fixed value for prey size (P) of 0.5mm approximates the size of the experimental microzooplankters and that of the common small copepod genera present in the Benguela system (De Decker 1984; Armstrong et al 1987; Hutchings 1988), e.g. *Oithona*, *Oncaea*, *Paracalanus* and *Ctenocalanus*. The range of plankton concentration (C) from 0 - 0.5 mgC. l^{-1} and the fixed value of 0.1 mgC. l^{-1} were estimated from the extensive net surveys reported in Hutchings (1988). Foraging times were set using the same assumptions as for phytoplankton.

TABLE 6: Minimum values of P, C and h derived from the budgets.

VARIABLE	FOOD TYPE: PHYTOPLANKTON	MICROZOOPLANKTON	MESOZOOPLANKTON
A) CARBON BUDGET			
P	0.20 mm	0.32 mm	0.61 mm
C	0.30 mg Cl^{-1}	0.03 mg Cl^{-1}	3.75 X 10^{-3} mg Cl^{-1}
h	7.5 $hrs.day^{-1}$	3.0 $hrs.day^{-1}$	0.2 $hrs.day^{-1}$
B) NITROGEN BUDGET			
P	0.29 mm	0.46 mm	0.77 mm
C	0.68 mg Cl^{-1}	0.06 mg Cl^{-1}	6.25 X 10^{-3} mg Cl^{-1}
h	15 $hrs.day^{-1}$	7.8 $hrs.day^{-1}$	0.55 $hrs.day^{-1}$

Mesozooplankton

Prey size was varied between 0.7mm - 3.0mm, since the former approximated the smallest prey length observed to elicit particulate feeding in *E.capensis* (0.711mm) and the latter approached the prey size at which the clearance rate (F) became independent of P (Chapter four). The fixed value of 2.0mm is similar to the adult sizes of common large copepoda found in the Benguela, such as *Calanus australis* and *Calanoides carinatus* (De Decker 1984; Hutchings 1988), which comprise a large portion of the anchovies' diet (Chapter two). Plankton concentrations were estimated from the most comprehensive mesozooplankton biomass data collected off the West coast of South Africa (Verheye and Hutchings 1988). The 0 - 8 hr. day^{-1} range in foraging time and the fixed value of 4 hrs. day^{-1} represent the main and peak feeding times respectively observed in St Helena Bay by James (Chapter two).

In Figs. 3 - 8, A_1 - C_1 detail the carbon or nitrogen intake and losses due to defaecation; A_2 - C_2 carbon and nitrogen expenditure; A_3 - C_3 net carbon or nitrogen intake and A_4 - C_4 growth and gross growth efficiency. In A_3 - C_3, the intersection between the lines representing absorbed ration (pR_C) and losses through respiration and excretion {(T_C + E_C) or E_N} indicates the minimum values of the three variables at which *E. capensis* may attain its daily maintenance ration (summarised in Table 6). The shaded

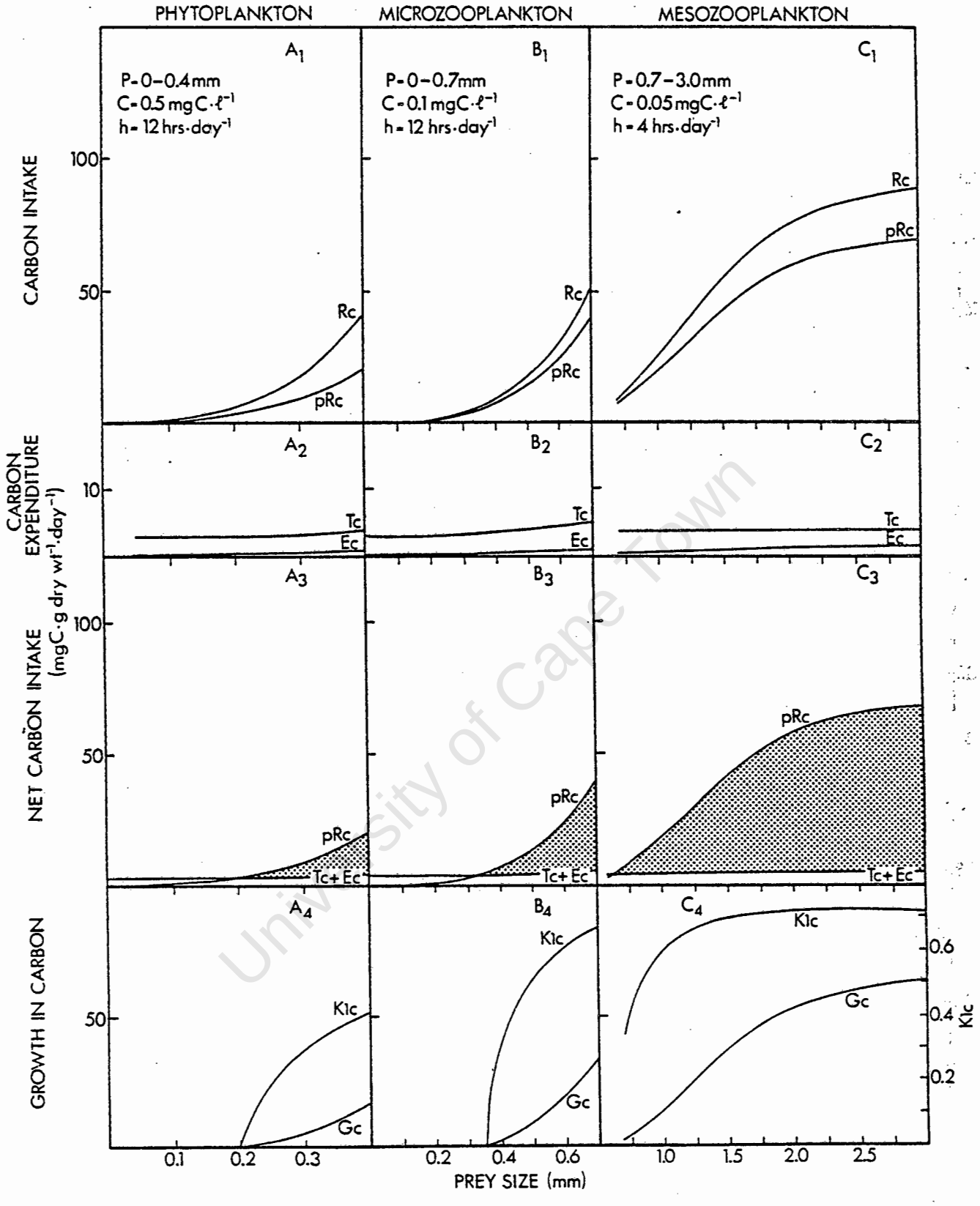


FIGURE THREE. The effect of prey size upon 1) intake, 2) expenditure, 3) scope for growth and 4) growth and growth efficiency of E. capensis feeding upon A) phytoplankton, B) microzooplankton and C) mesozooplankton.

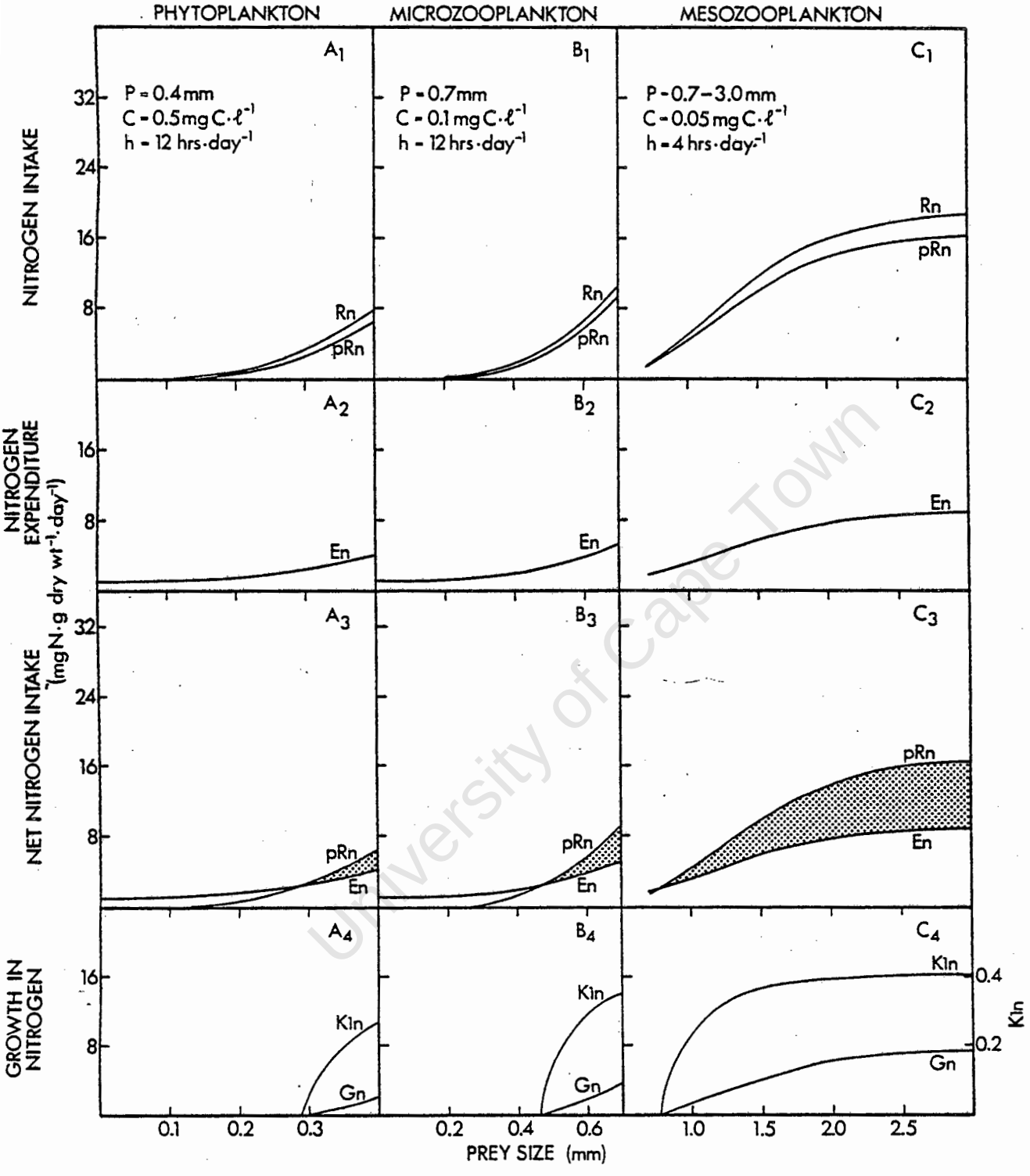


FIGURE FOUR. The effect of prey size upon nitrogen 1) intake, 2) expenditure, 3) scope for growth and 4) growth and growth efficiency of E. capensis feeding upon A) phytoplankton, B) microzooplankton and C) mesozooplankton.

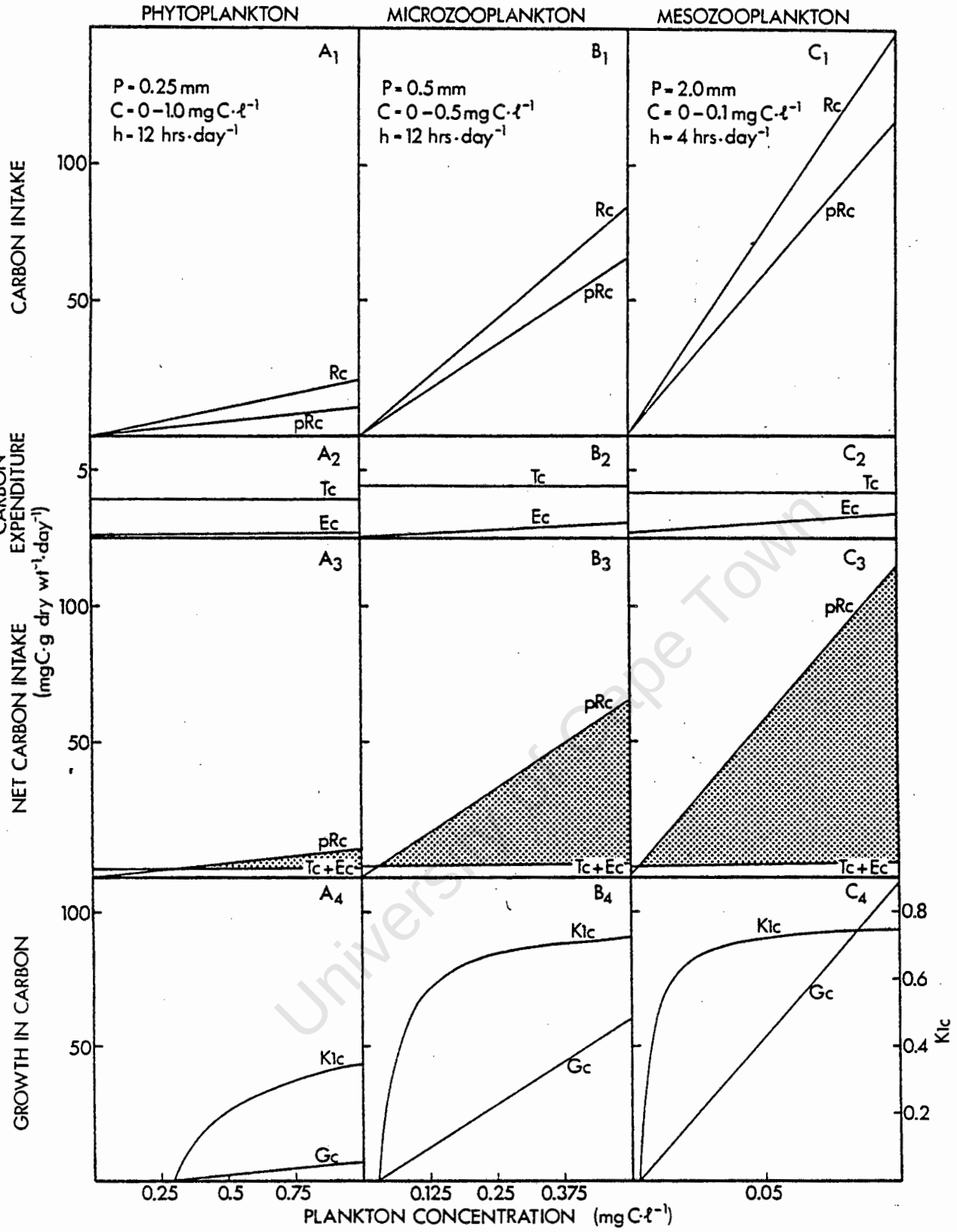


FIGURE FIVE. The effect of plankton concentration upon the outputs of the carbon budgets derived for E. capensis. The labelling is identical to that used in Fig. 3.

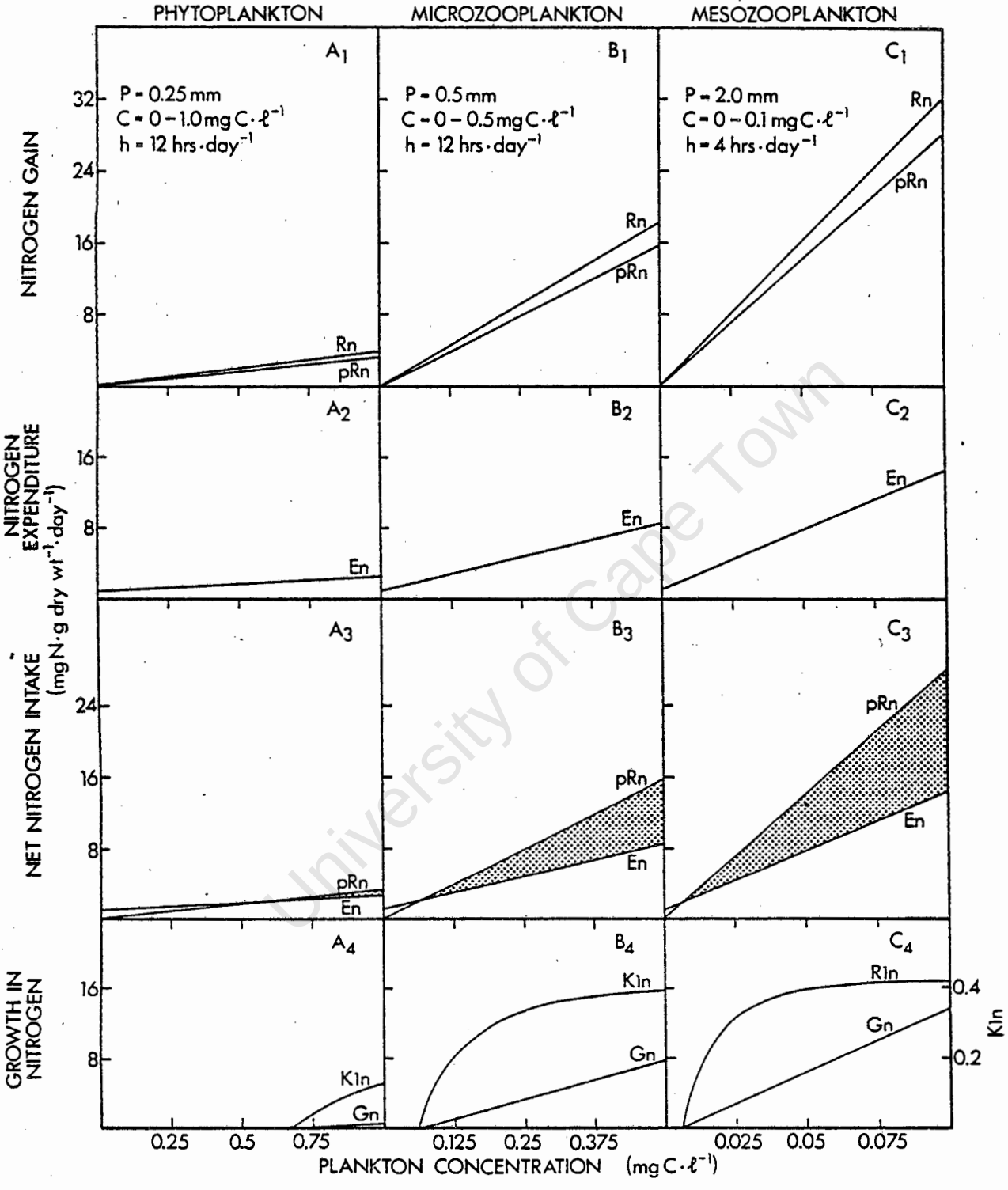


FIGURE SIX. The effect of plankton concentration upon the outputs of the nitrogen budgets derived for E. capensis. The labelling is identical to that used in Fig. 4.

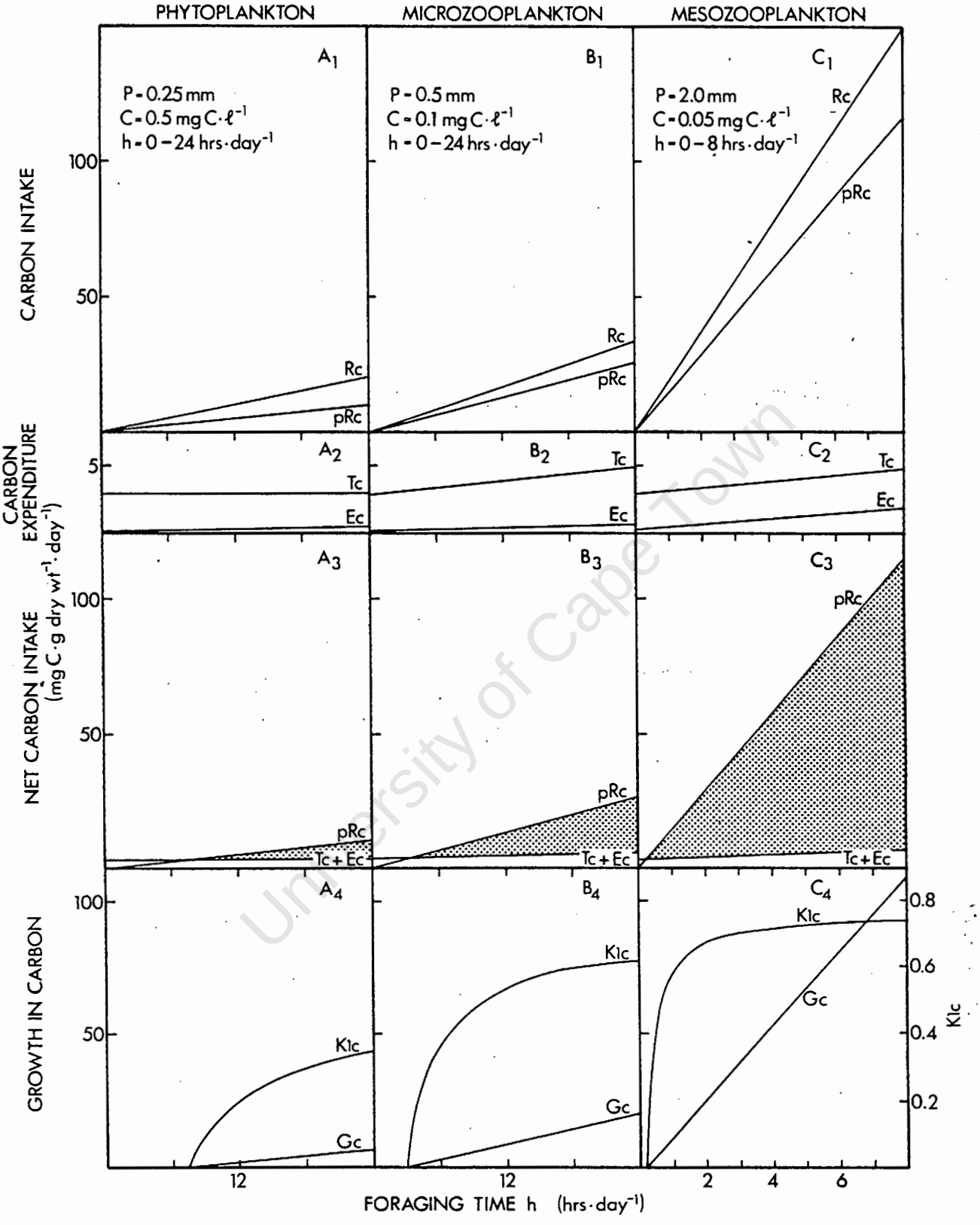


FIGURE SEVEN. The effect of foraging time upon the outputs of the carbon budgets derived for E. capensis. The labelling is identical to that used in Fig. 3.

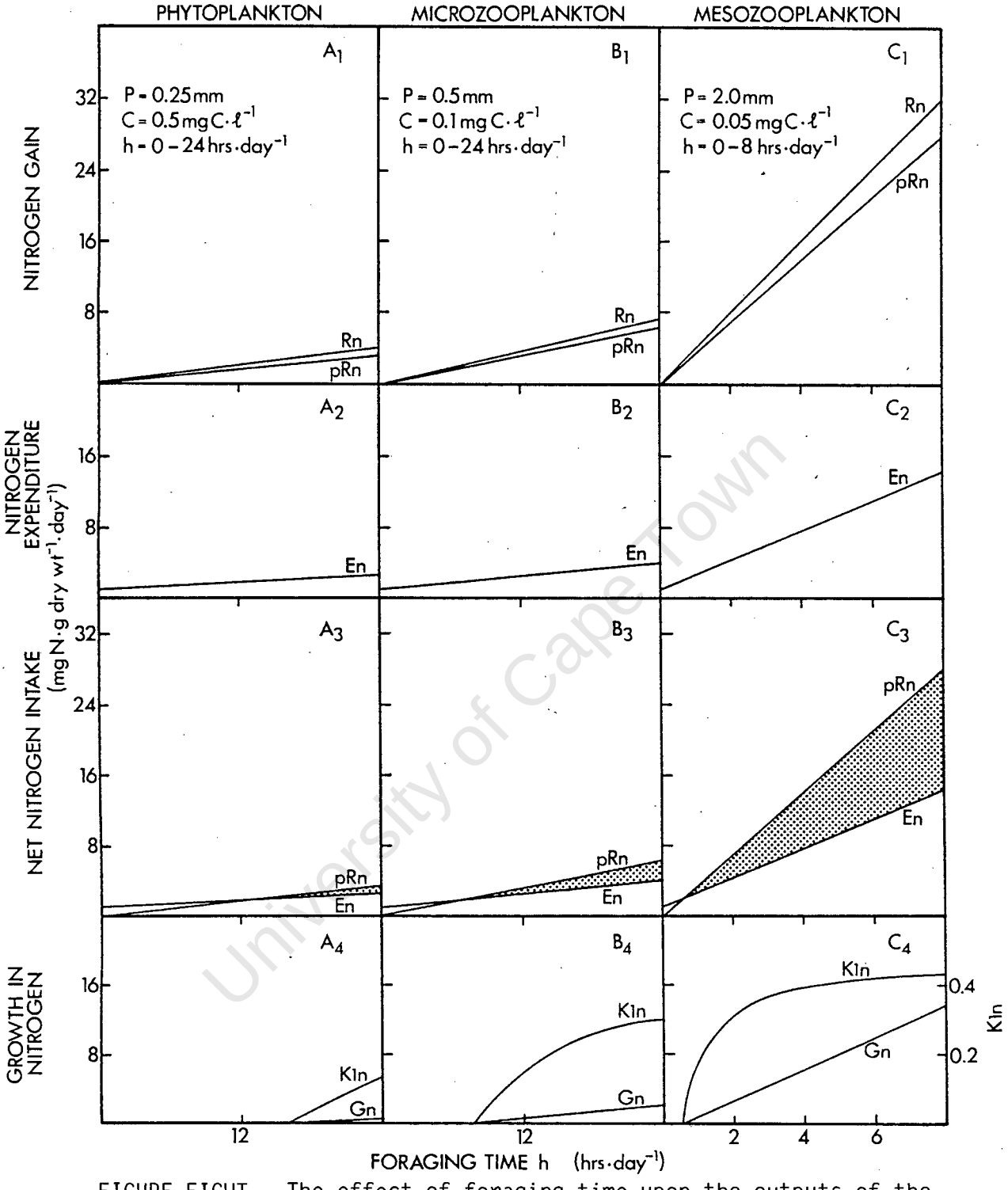


FIGURE EIGHT. The effect of foraging time upon the outputs of the nitrogen budgets derived for E. capensis. The labelling is identical to that used in Fig. 4.

areas represent the scope for growth and reproduction under the conditions described.

When prey size (P) was varied and plankton concentration (C) and foraging time (h) held constant (Figs. 3 and 4, A - C), the ingested ration, assimilated ration, the losses through respiration and excretion and growth increased exponentially when phytoplankton or microzooplankton was the food and asymptotically when mesozooplankton was the food. The gross growth efficiency always increased asymptotically.

When plankton concentration (C) was varied and prey size (P) and foraging time (h) remained constant (Figs. 5 and 6, A - C), all model outputs increased linearly with increasing plankton concentration, except respiration , which remained constant (since both P and h were fixed), and the gross growth efficiency, which increased asymptotically.

In Figs. 7 and 8, A - C, when foraging time (h) was varied while prey size (P) and plankton concentration (C) remained fixed, all outputs increased linearly with increasing foraging time, except the gross growth efficiency, which increased asymptotically.

The examples demonstrate that the relative magnitude of each component of the carbon and nitrogen budgets varies according to the values of prey size (P), plankton concentration (C) and

foraging time (h). The curvilinear relationships between the components of the carbon and nitrogen budgets and prey size (Fig 3 and 4) are due to the non linear functions describing the effect of prey size upon two major inputs into the models - the clearance rate (F) and the swimming speed (s). When prey size is fixed, the relationships are linear since plankton concentration and foraging time have a direct proportional effect upon the model outputs (Fig 5, 6, 7 and 8).

Carbon losses through respiration were similar for all three budgets (Fig 3, 5 and 7 A_2 - C_2). Yet the ingested ration increased dramatically as the prey size increased, despite the fact that prey size was the major influence upon both components (Fig 3, 5 and 7 A_1 - C_1 and A_2 - C_2). These observations illustrate the difference between the functions governing the relations between prey size and clearance rate and swimming speed respectively (equations 5 and 23). Small prey sizes, which elicit the filtering response from *E. capensis*, cause large increases in swimming speed, but have little effect on the clearance rate (Figs. 1 and 2). Larger prey which elicit the particulate feeding response, cause large increases in the feeding rate, but have little effect upon the swimming speed (Figs. 1 and 2). Thus, during filter feeding, increases in prey size cause a large increase in carbon expenditure through respiration relative to the increase in gain. In contrast, during particulate feeding the oppposite is the case and increments in prey size result in large increases in carbon

gain relative to expenditure. This point is best illustrated by an example:

an increase in prey size from 0.25 - 0.7mm during filterfeeding causes an increase in swimming speed and respiration rate of 17.38 - 24.86 cm.s^{-1} and 0.115 - 0.237 mgO_2.g wet wt^{-1}.hr^{-1} respectively, whilst the clearance rate increases from 0.07-0.42 l.fish^{-1}.min^{-1}. A similar increase during particulate feeding from 0.7 - 1.2 mm causes increases in swimming speed and respiration rate of 24.86 - 27.61 cm.s^{-1} and 0.249 - 0.291 mgO_2.gwet wt^{-1}.hr^{-1} respectively and the clearance rate increases from 0.42 - 7.02 l.fish^{-1}.min^{-1}.

An important aspect illustrated by the budgets developed, is that there are minimum conditions which must be met before *E. capensis* can achieve its maintenance ration (Figs 3 - 8, A_3 - C_3). For any plankton concentration and foraging time, there is a minimum prey size (Figs. 3 and 4 A_3 - C_3). Similarly there are minimum plankton concentrations and foraging times for any combination of prey size and foraging time and prey size and plankton concentration respectively (Figs 5 and 6, and 7 and 8, A_3 - C_3). This observation leads to two conclusions concerning the budgets. Firstly, there can be no standard carbon and nitrogen budgets for *E. capensis* since the three variables are independent and bear no fixed relation to each other. Durbin and Durbin (1983) arrived at a similar conclusion after developing energy and nitrogen budgets for *Brevoortia tyrannus* using foraging speed, plankton concentra-

tion and foraging time as variables. Secondly, in order for *E. capensis* to show positive growth in either carbon and nitrogen, the minimum values of prey size, plankton concentration and foraging time must be exceeded (summarised in Table 6).

The minuimum value of prey size for phytoplankton is similar to the minimum size that *E. capensis* is capable of filtering as estimated in Chapter four, whilst that for mesozooplankton approximates the threshold size of ± 0.7 mm when the anchovy switches from filter to particulate feeding. The minimum plankton concentrations for phytoplankton and microzooplankton are considerably greater than the threshold concentrations observed in Chapter four for the initiation and termination of filterfeeding, indicating that E. capensis may filterfeed even when it is uneconomical to do so. James (Chapter four) observed gaping behaviour in anchovy in the absence of food. It is possible that the filtering response observed during the initiation trials was no more than the anchovy testing the water for the presence of suitable food, as suggested by Durbin and Durbin (1975) for *Brevoortia tyrannus*. The minimum value of C for particulate feeding is only 3.75×10^{-3} mgC. l^{-1} (Table 6). This explains why threshold concentrations for neither the initiation nor the termination of particulate feeding activity were ascertained in Chapter four, since such low concentrations were beyond the limits of the experimental design.

These minimum values are products of the gains and expenditures resulting from the utilisation of the various food types. They indicate that under the conditions that prevail in the southern Benguela system, (see Table 5 and explanation in text) *E. capensis* could attain its maintenance ration in both carbon and nitrogen most easily by particulate feeding upon mesozooplankton. Particulate feeding upon mesozooplankton also provides for the largest scope for growth, fastest growth rates and highest growth efficiencies (Figs 3 - 8, A_3 - C_3 and A_4 - C_4). It is interesting that during particulate feeding, intake, growth rates and growth efficiency are maximal over most of the range of prey size, including such preferred prey items as large copepods, amphipods and euphausiids (Chapter two).

In all instances, larger prey sizes, higher plankton concentrations and longer foraging times are required to fulfill the maintenance rations for nitrogen than for carbon and growth and growth efficiencies are lower for nitrogen than carbon. Thus, *E. capensis* is capable of positive growth in carbon under conditions when growth in nitrogen is impossible, suggesting that nitrogen may be a factor limiting the growth potential of anchovy in the wild.

DISCUSSION

The carbon and nitrogen budgets presented here were developed in a similar fashion to the energy and nitrogen budgets derived by Durbin and Durbin (1983) during their landmark study of the bioenergetics of the filterfeeding planktivore *Brevoortia tyrannus*. However there are several fundamental differences. Durbin and Durbin (1983) utilised theoretical values for the volume searched by and the feeding efficiency of *B. tyrannus*. During the present study, clearance rates by *E. capensis* feeding upon a range of particle sizes were measured experimentally. In the development of their energy and nitrogen budgets, Durbin and Durbin (1983) used foraging speed, plankton concentration and foraging time as their variables and investigated the effects upon the bioenergetics of B. tyrannus feeding on a single food type and size (the solitary diatom *Ditylum brightwelli*, mean size 0.070 mm diameter). Following the work of Ware (1975 and 1978) they calculated the optimal foraging speeds of the fish feeding upon this food over a range of plankton concentrations and foraging times. In the present study prey size was employed as a variable, instead of foraging speed, since it was found that the former influenced the latter.

I believe that there are several advantages associated with my approach, compared to that of earlier work (Werner and Hall 1974; O' Brien et al 1976; Eggers 1977; Ware 1975, 1978 and Durbin and Durbin 1983). Firstly it is difficult to apply previous models to

field conditions, since it is virtually impossible to measure such theoretically defined parameters as volume searched and feeding efficiency, even under laboratory conditions, and it is also impractical to assume that acoustic measurements of fish foraging speeds can be obtained in the field to the degree of accuracy required by the models. On the other hand, the clearance rate of any particle is relatively easily quantified in the laboratory (Chapter four) and prey size is easily measured under field conditions (Chapter two). Thus all three variables employed in the present budgets may be collected routinely from plankton hauls and fish trawls (Chapter two) and utilised to determine the potential growth of *E. capensis* in the field on a regular basis. The derivation of optimal foraging speeds for *E. capensis* may be of limited ecological significance. James (Chapter four) found that the swimming speeds of anchovy feeding upon phytoplankton, microzooplankton and mesozooplankton were significantly different from each other. But for each food type the swimmming speed was relatively consistent over a wide range of concentrations. The results of the carbon budgets also suggest that *E. capensis* reacts to prey size by altering its swimming speed to reduce expenditure and enhance growth and growth efficiency, rather than to plankton concentration. This implies that for any prey size there is a swimming speed that optimises the intake versus the expenditure for the anchovy. Thus, the optimal foraging speeds of earlier budgets calculated for a single prey size are incorporated into the present budgets, which have been taken one

step further to assess the reaction of a planktivore to the size assemblage of available prey. This is an important step since prey size has been shown to be the primary influence upon both the feeding behaviour and the rates of intake and expenditure in *E. capensis*. Furthermore, changes in size assemblage of prey are likely to be more frequent and marked than changes in total plankton concentration.

The budgets developed clearly illustrate the superior economy and cost effectiveness of particulate feeding compared to filter feeding under the trophic conditions prevalent in the Southern Benguela. It is concluded from this study that *E. capensis* obtains the bulk of its nutritional requirements by particulate feeding upon meso - and macro - zooplankton. This income may be supplemented by filterfeeding upon dense concentrations of phyto- and micro - zooplankton. The results of the field and experimental studies employed to develop these budgets and the budgets themselves reject the findings and hypotheses of the earlier studies of Robinson (1966), King and MacCloed (1976) and Cruikshank (1987) who stated that *E. capensis* is sustained primarily by filterfeeding upon the abundant diatom chains present in its environment. The budgets indicate that phytoplankton densities only slightly lower than those of bloom conditions are required to maintain the anchovies' carbon and nitrogen balances and that even at very high phytoplankton concentrations growth is limited. This potential for growth upon a phytoplankton diet is further

limited when it is realised that *E. capensis* is only capable of filtering particles with an apparent size of greater than approximately 0.2 mm from the water. This renders most of the primary production in the environment inaccessible to the anchovy (Chapter four), especially when microflagellates dominate the phytoplankton community. James (Chapter two) only observed phytoplankton to contribute significantly to the daily diet of *E. capensis* when dense concentrations of large *Coscinodiscus* spp cells were present. Even under these conditions, its total contribution was limited. The relative importance of the contribution of phytoplankton to fulfilling the daily maintenance and growth requirements of *E. capensis* may vary with area. In the northern Benguela region, where blooms of large robust chains of *Delphineus* spp are common, its contribution to the carbon and nitrogen balances may be more significant. However, as a general rule, phytoplankton's direct contribution towards meeting the nutritional requirements of E. capensis can be considered to be small compared to the input from zooplankton and at best is a minor source of additional income through a "by-catch" of diatom chains as the anchovy pursue their preferred meso - and macro - zooplankton prey.

Filterfeeding upon microzooplankton produces a slightly more profitable scenario than that of phytoplankton, but again this food source may be considered to be secondary to meso - and macro - zooplankton. It only being of consequence when the anchovy encounters dense aggregations of small zooplankters in the

Appendix A

Personal communication from F. Schülein.

A FIELD OBSERVATION ON THE FEEDING BEHAVIOUR OF *SARDINOPS OCELLATA*.

During the fifties and mid-sixties, when pilchard were still abundant in Southwest Africa/ Namibia, it frequently happened that shoals of this species entered the harbour area of Walvis Bay (23°00'S', 14°30'E). Here they were captured with ease, for tagging and further research purposes during the closed fishing season between October and March (summer - autumn), or for commercial purposes during winter and spring. Cases have been observed where catches, taken alongside offloading jetties, were pumped directly from the purse seine into the factory plant, or where hunting snoek (*Thyristes atun*) forced pilchard shoals to the surface , thereby pressing part of the shoal above the water surface which were then visible as a dense layer of thrashing and "dry" fish (Matthews pers. comm.). Such observations were mostly made during the closed seasons or at the start of the fishing activities when pollution of the bay was usually low.

Under such conditions in early 1963 I, by chance, observed a loose and scattered shoal of about 500 - 700 adult pilchard feeding at the water surface next to the jetty of the local research Institute. These fish, spread over an area of about 2m -

3m in diameter, haphazardly and vigorously moved about at distances of about 10cm - 30cm apart, with their mouths and opercula widely expanded (like wings), and each fish breaking the water surface. In fact, a rustling noise first attracted my attention when passing these fish at a distance of about 5m on the jetty. This occurrence was at about 10.00 hrs. in bright sunlight. The water was clear and unpolluted, and no wind was blowing.

The fish were obviously feeding upon zooplankton. However, no samples or further evidences were collected as it was believed that such observations were well documented. Similar, but less spectacular observations were also occasionally made on juvenile mullets (*Mugil* spp.) which, during summer, regularly occurred in small shoals underneath the jetties in the Bay.

The feeding performance of these pilchard lasted for some 10 minutes after they were first observed. During this period, the fish stayed within their scattered shoal which, at one stage, passed underneath the jetty but then returned to the region where they were first seen. At this later stage their numbers were apparently still the same, but then rapidly declined when the fish submerged in a rather scattered fashion, all bearing in a northerly direction.

It would be rather strange if nobody else has made any similar observations thus far.

Appendix B

COMPOSITION OF THE ARTIFICIAL FOOD USED TO FEED WILD *ENGRAULIS CAPENSIS* BEING MAINTAINED IN THE LABORATORY.

INGREDIENTS	COMPOSITION g / Kg
BEEF LIVER / FROZEN ANCHOVY / ROCK LOBSTER OFFAL	694
COMMERCIAL TROUT PELLETS	140
WATER	140
GELATINE	25.5
VITAMIN C	0.5
TRACE INGREDIENTS	I.U. or mg / Kg
VITAMIN A	1700 I.U.
B1	0.5 mg
B2	0.7 mg
D3	150 I.U.
E	0.8 mg
NICOTINAMIDE	5.0 mg
MANGANESE SULPHATE	2.1 mg
POTASSIUM IODIDE	TRACE

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